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A synopsis of the numbers of testicular follicles and ovarioles in true bugs (Heteroptera, Hemiptera) – sixty-five years of progress after J. Pendergrast's review

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Abstract

The structure of testes and ovaries can be described in its simplest form by the number of follicles and ovarioles they contain. Sixty-five years after the last review of the internal reproductive systems in true bugs (Heteroptera), the data accumulated today on the number of testicular follicles and ovarioles in their gonads are summarized. In addition, data on the number and type (mesadenia/ectadenia) of accessory glands are given. The hemipteran suborder Heteroptera constitutes one of the most diverse groups of non-homometabolous ('Hemimetabola') insects, comprising more than 40,000 described species worldwide and approximately 100 families, classified into seven infraorders. Data are available for all infraorders; however, more than 90% of studied species belong to the largest and most evolutionarily derived infraorders Cimicomorpha and Pentatomomorpha. In true bugs, in general, the number of follicles varies from one to nine (in a testis), and the number of ovarioles varies from two to 24 (in an ovary). Seven follicles per testis and seven ovarioles per ovary prevail being found in approximately 43.5% (307 species) and 24.4% (367 species) of studied species, respectively. Such a structure of testes and ovaries is considered an ancestral character state in the Heteroptera. In the evolution of this group, the number of follicles and ovarioles both increased and decreased, but the trend towards a decrease clearly prevailed.

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Keywords
Accessory glands, ectadenia, evolution, mesadenia, ovarioles, phylogeny, testicular follicles, true bugs

Introduction

The hemipteran suborder Heteroptera (or true bugs) displays remarkable morphological variation and comprises more than 40,000 described species worldwide in ~ 100 families classified into seven infraorders including Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha, and Pentatomomorpha. The majority of true bug species are herbivorous but some are predators and blood-suckers (Štys and Kerzhner 1975; Henry 2009; Schuh and Weirauch 2020).

The internal anatomy of the true bug males and females has been investigated for nearly two centuries. The first report on this topic appeared in the thirties of the 19th century (Dufour 1833). Substantial comparative research on the internal anatomy of true bugs had accumulated by the 1960s mostly as a consequence of publications by J. Carayon, D. Leston, S. Miyamoto, T.E. Woodward, and J.G. Pendergrast (see Pendergrast 1957 and Miyamoto 1957 for references). Pendergrast (1957) published the first and, up to the present time, the only review of data available by that time on the internal reproductive organs of true bugs. Overall, Pendergrast summarized the literature (~ 90 titles) and his own data on ~ 50 families of Heteroptera and also shortly commented on the value of different parts of the male and female reproductive organs as characters in the taxonomy and classification of the Heteroptera. Despite the fact that Pendergrast singled out some organs as potentially promising for these purposes (in particular, testes in terms of the number of follicles they contain), he concluded that there is still very little data to make any generalizations. A huge contribution was made by Miyamoto (1957), who summarized the literature and own data on the structure of the ovaries in almost 300 representatives of ~ 40 families (some of them no longer families and other subfamilies recently erected to the separate families). Since the Pendergrast's overview and Miyamoto's list, ~ 120 original articles concerning the internal reproductive organs of Heteroptera have been published. In most cases, studies concern single species, and comparative data across multiple species of a group are few (e.g., Kumar 1967: Aradidae; Leston 1961a; Leston and Gibbs 1968; Malipatil 1978: Lygaeidae; Akingbohungbe 1983: Miridae; Grozeva and Kuznetsova 1992: Aradidae, Piesmatidae, Berytidae, Lygaeidae, Pyrrhocoridae). Much valuable information on true bugs can be found in special monographic works devoted to the reproductive systems of insects in general (Matsuda 1976; Büning 1994a, b; Chapman et al. 2013; Klowden 2013).

Although there is considerable diversity in detail, the internal parts of the male and female reproductive systems are organized similarly in different insects. In males of true bugs, it is formed by a pair of testes consisting of a variable number of testicular follicles, two different ducts, a median ejaculatory duct, and accessory glands. Accessory glands may be ectodermal or mesodermal in origin being known as ectadenia or

mesadenia, respectively. Ectadenia open into the ejaculatory duct, whereas mesadenia open into the vasa deferentia or the distal end of the ejaculatory duct. In some species, both ectadenia and mesadenia are present, while other species have no accessory glands at all (Pendergrast 1957; Suppl. material 1). In females, the reproductive system is formed by a pair of ovaries consisting of a variable number of ovarioles, two lateral oviducts, a median common oviduct, and a spermatheca. The ovarioles are known to be of the meroistic telotrophic type (Chapman et al. 2013). In some species, accessory glands may also be present.

During the years that have passed since the aforementioned overviews, the number of species and higher taxa of true bugs studied in relation to testes and ovaries has almost tripled, and it seems appropriate to publish an updated list. In this review article, all the data available today, including new data on 140 species obtained by the authors, are summarized in two tables. Suppl. material 1 includes all species studied to date in terms of the number of follicles and ovarioles. In some cases, additional information, e.g., on the number and type of accessory glands (ectadenia or mesadenia) in the male reproductive system, is also provided. Table 1 summarizes data presented in Suppl. material 1 and shows the variability of the number of follicles and ovarioles at different taxonomic levels, together with the modal values for each of the higher taxa explored. On Fig. 1, the internal reproductive organs of a male and a female of *Arocatus longiceps* Stål, 1872 (Lydaeidae) is given. In Figs 2 and 3, character states of testicular follicle and ovariole numbers, respectively, are mapped onto the phylogenetic tree of Heteroptera families taken from Weirauch et al. (2019). In the final section of the review, the diversity of the analyzed characteristics and main tendencies of their evolution in true bugs are discussed. We hope that our review will be of importance for future work on the diversity of reproductive morphology within the Hemiptera, and that the data may provide additional information for understanding relationships between the higher taxa of true bugs.

Materials and methods

The current review article is part of a long-term research project dedicated to the study of true bugs, including the morphology of their reproductive system, cytogenetics, and evolution. The data we have obtained over years on the structure of testes and ovaries of true bugs in terms of the number of testicular follicles and ovarioles constitute at the present time a significant part of all such data currently available for the Heteroptera in general (Suppl. material 1). The material was collected during the expeditions of the authors (1986–2021) or provided by colleagues, mainly by D. Gapon, L. Hill, and H. Gunther. Material comes from different regions of Palaearctic (Europe: predominantly southern Europe and the Balkans, Central Asia, Caucasus) and some parts of the Old Tropics (Vietnam, Indonesia, Himalayas, India, Thailand, Tasmania). Species identification was made by authors or collectors (in case of donated material). Voucher samples are deposited in the insect collections of the National Museum of Natural

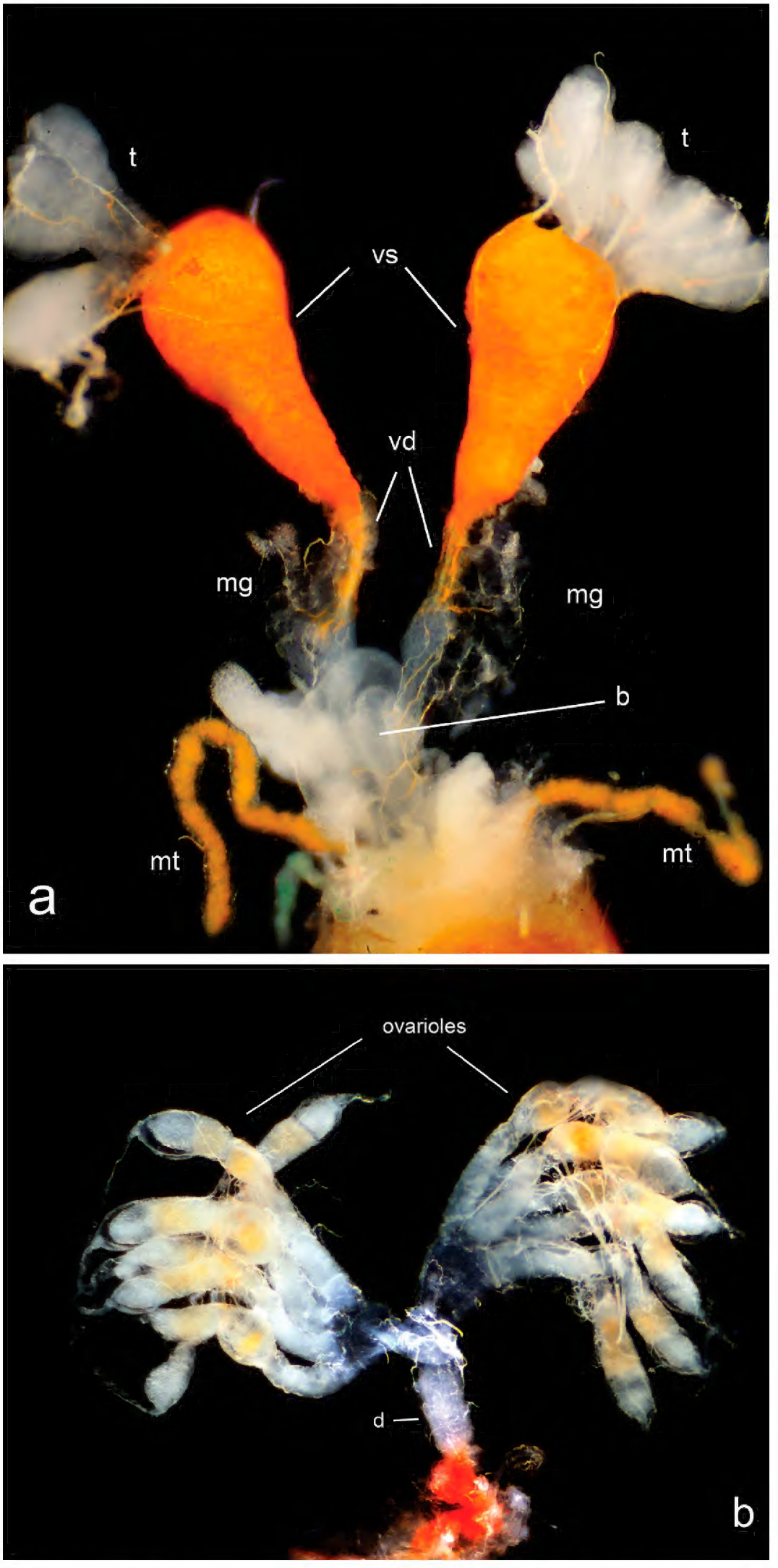

Figure 1. a Male (seven follicles) and **b** female (seven ovarioles) reproductive systems of *Arocatus longiceps* Stål, 1872 (Lygaeidae). Abbreviations: t – testis, vd – vas deferens, vs – vesicula seminalis, mg – mesadenia, b – bulbus, mt – malpighian tubule, d – ductus (spermatheca and accessory glands were not visible in females).

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Our original data cover 140 species belonging to 30 families, six infraorders, and represent 13.8% of all data on the structure of the testes and ovaries of true bugs accumulated to date and presented in Suppl. material 1. Some of these data have been published previously, the other part is presented here for the first time. Our study was carried out on specimens fixed in Carnoy fixative (3:1 96% ethanol and glacial acetic acid) that allowed both morphological and chromosomal analyses of the same individual. Material fixed in Duboscq Brasil (alcoholic Bouin's) and ethanol (95%) was also used. The gonads were dissected out of the abdomen in a drop of 45% acetic acid on a microscope slide. The testicular follicles of the male and the ovarioles of the female were carefully separated from each other and counted under a stereomicroscope. Other parts of the reproductive system have also been studied, most notably, the accessory glands in males.

Classification used in this work follows Schuh and Weirauch (2020) except for Micronectidae which are treated as a separate family due to distinct cytogenetic features (Grozeva et al. 2008) and following Nieser (2002). All taxa are listed alphabetically.

Numbers of testicular follicles and ovarioles were treated as unordered states of two hidden characters and optimized on the Bayesian total-evidence tree of Heteroptera published by Weirauch et al. (2019) with all terminals of the original topology collapsed to family level. The phylogenetic reconstruction of Weirauch et al. (2019) was chosen for character mapping as the most recent analysis of the entire Heteroptera employing comprehensive coverage of true bug families. The data recorded in this publication comes from all available literature (Dufour 1833; Gross 1901; Marshall and Severin 1903; Bowen 1922a, b; Kerkis 1926; Ludwig 1926; Poisson 1927; Sarel-Whitfield 1929; Wille 1929; Hagan 1931; Payne 1934; Baumgartner and Witherspoon 1937; Kirkpatrick 1937; Larsen 1938; Slack 1938; Schneider 1940; Kullenberg 1947; Carayon 1949, 1950, 1951, 1954, 1955, 1972; Woodward 1949, 1950, 1977; Bonhag and Wick 1953; Davis 1955, 1956, 1966, 1970; Pendergrast 1956, 1957; Miyamoto 1957, 1959; Scudder 1957; Barth 1958; Usinger and Matsuda 1959; Drake and Davis 1960; Schrader 1960a; Leston 1961a, b; Kumar 1962, 1964, 1965, 1967, 1969; Slater and Miyamoto 1963; Bhargava 1967; Leston and Gibbs 1968; Brunt 1971; Kauffman 1971; Huebner and Anderson 1972; Louis and Kumar 1973; Wightman 1973; Jansson and Scudder 1974; Malipatil 1978; Lung and Goeden 1982; Akingbohungbe 1983; Heming-van Battum and Heming 1986, 1989; Gonçalves et al. 1987; Ma and Ramaswamy 1987; Postle and Woodward 1988; Grozeva and Kuznetsova 1989, 1992; Socha et al. 1988; Papáček and Gelbič 1989; Biliński et al. 1990; Jawale and Ranade 1990; Gelbič et al. 1991; Hunt and Stebbing 1992; Papáček and Soldán 1992, 2008; Lent et al. 1994; Grozeva 1995, 2003, 2007; Grozeva and Nokkala 1996, 2001; Simiczyjew et al. 1996, 1998; Lalitha et al. 1997; Papáček et al. 1997; Štys et al. 1998; Simiczyjew 1999; Adams 2001; Couturier et al. 2002; Lis 2003; Kuznetsova et al. 2004, 2007; Lemos et al. 2005a, b, 2010; Santos et al. 2005; Grozeva et al. 2006, 2007, 2008, 2009, 2013; Jahnke et al. 2006; Kugler

et al. 2006; Freitas et al. 2007a, b, 2008, 2010, 2012; Mróz 2007, 2012; Ogorzałek 2007; Pires et al. 2007; Grozeva and Simov 2008; Esquivel 2009; Marchini et al. 2009; Ogorzałek and Trochimczuk 2009; Souza et al. 2009; Chiang 2010, 2013; Van Doesburg et al. 2010; Horton and Lewis 2011; Mróz and Wojciechowski 2011; Souza et al. 2011, 2014; Uceli et al. 2011; Chiang et al. 2012; Kaur and Patial 2012, 2016; Soto et al. 2012; Gomes et al. 2013; Özyurt et al. 2013a, b, 2014a, b, 2015; Pluot-Sigwalt and Chérot 2013; Jyoti et al. 2015; Pereira et al. 2015; Cremonez et al. 2017, 2019; Elelimy et al. 2017a, b; Novais et al. 2017; Candan et al. 2018; Mahmood et al. 2018; Grodowitz et al. 2019, 2020; Khandelwal et al. 2019; Koçakoğlu et al. 2019; Xia 2019; Araújo et al. 2020a, b, 2021; Munhoz et al. 2020, 2021; Vélez et al. 2020; Gapon 2021; Oliveira et al. 2021; Bugaj-Nawrocka et al. 2022; Koutsogeorgiou et al. 2022; Samanta et al. 2022), and original observations (see Suppl. material 1).

The coding strategy aimed at reflecting diversity in numbers of follicles per testis (hereafter p.t.) and ovarioles per ovary (hereafter p.o.) observed within a given family. Therefore, states were coded as polymorphic in cases of large variability of follicle and ovariole numbers within a given family. This was the case for large and comparatively well studied families lacking widely accepted phylogenetic resolution e.g., Aradidae, Miridae, or Pentatomidae. However, in groups with a robust backbone phylogeny in place, e.g., Reduviidae (Weirauch 2008; Weirauch and Munro 2009; Hwang and Weirauch 2012), there was no doubt that the testis follicle number of seven is not only most common across the family, but may be treated as ancestral, and was coded as such. Within Veliidae, *Halovelia septentrionalis* Esaki, 1924 remains the only veliid species having two ovarioles p.o. Phylogeny of Gerromorpha by Damgaard (2008) rendered Haloveliinae as a sister group to Microveliinae which in turn forms a sister group to Gerridae. All veliid taxa including the second studied haloveliine species have four ovarioles p.o. and therefore we consider this number as an ancestral state for all veliids. History of both characters was traced using Mesquite 3.6.1 (Maddison and Maddison 2018) with the parsimony ancestral state reconstruction method (Figs 2, 3).

Results and discussion

In this work, we have compiled ~ 1200 records of the numbers of testicular follicles and ovarioles in 1008 true bug species from across 63 families and seven infraorders, including Enicocephalomorpha (one family, two species), Dipsocoromorpha (three families, twelve species), Nepomorpha (eleven families, 50 species), Gerromorpha (five families, 50 species), Leptopodomorpha (two families, five species), Cimicomorpha (12 families, 474 species), and Pentatomomorpha (29 families, 437 species). Below we will comment on the available data for each infraorder, with emphasis on those families in which such data are more or less representative. Data on male accessory glands, their numbers, and origins (mesadenia/ectadenia), although provided in Suppl. material 1, are not specifically discussed since they are still very few.

Table 1. Distribution of numbers of follicles and ovarioles by families (Summarized based on Suppl. material 1).

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Cimicomorpha	**Anthocoridae**			**20**		**1**			**3**								**6**			
Cimicomorpha	Anthocoridae	Almeidini							1								1			
Cimicomorpha	Anthocoridae	Anthocorini		10		1											1			
Cimicomorpha	Anthocoridae	Blaptostetini		1																
Cimicomorpha	Anthocoridae	Cardiastethini		6													1			
Cimicomorpha	Anthocoridae	Oriini		1													2			
Cimicomorpha	Anthocoridae	Scolopini		2																
Cimicomorpha	Anthocoridae	Xylocorini							2								1			
Cimicomorpha	**Cimicidae**	**Cimicinae**							**2**								**4**			
Cimicomorpha	**Joppeicidae**			**1**											**1**					
Cimicomorpha	**Lasiochilidae**			**2**													**1**			
Cimicomorpha	**Lyctocoridae**			**3**													**4**			
Cimicomorpha	**Microphysidae**		**1**																	
Cimicomorpha	**Miridae**	**23 tribes**	**26**	**60**	**58**	**1**		**3**	**72**	**10**		**1**	**1**				**36**	**7**		
Cimicomorpha	Miridae	Bryocorinae (Bryocorini)	3	2																
Cimicomorpha	Miridae	Bryocorinae (Dicyphini)	14	2													12			
Cimicomorpha	Miridae	Bryocorinae (Eccritotarsini)															1			
Cimicomorpha	Miridae	Bryocorinae (Felisacini)	2																	
Cimicomorpha	Miridae	Bryocorinae (Monaloniini)		2	3															
Cimicomorpha	Miridae	Cylapinae (Fulviini)	1						1											
Cimicomorpha	Miridae	Deraeocorinae (Deraeocorini)	2	3					2	7								1		
Cimicomorpha	Miridae	Deraeocorinae (Hyaliodini)		2																
Cimicomorpha	Miridae	Isometopinae (Isometopini)															1			
Cimicomorpha	Miridae	Mirinae (Hyalopeplini)															1			
Cimicomorpha	Miridae	Mirinae (Mirini)		1				1	61	3							12	3		
Cimicomorpha	Miridae	Mirinae (Stenodemini)	1	1	4			2	6								5	3		
Cimicomorpha	Miridae	Orthotylinae (Ceratocapsini)		4																
Cimicomorpha	Miridae	Orthotylinae (Coridromini)	1																	
Cimicomorpha	Miridae	Orthotylinae (Halticini)	1	2	5												1			
Cimicomorpha	Miridae	Orthotylinae (Nichomachini)			1															

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**17**	**24**
Cimicomorpha	Miridae	Orthotylinae (Orthotylini)	1	40									1				2			
Cimicomorpha	Miridae	Phylinae (Cremnorrhini)			5				1											
Cimicomorpha	Miridae	Phylinae (Hallodapini)			1				1											
Cimicomorpha	Miridae	Phylinae (Nasocorini)			6															
Cimicomorpha	Miridae	Phylinae (Phylini)			28	1								1						
Cimicomorpha	Miridae	Phylinae (Pilophorini)		1	4												1			
Cimicomorpha	Miridae	Phylinae (Semiini)			1															
Cimicomorpha	**Nabidae**	**5 tribes**			**1**				**16**			**1**					**19**			
Cimicomorpha	Nabidae	Nabinae (Arachnocorini)			1												1			
Cimicomorpha	Nabidae	Nabinae (Gorpini)															1			
Cimicomorpha	Nabidae	Nabinae (Nabini)							12								10			
Cimicomorpha	Nabidae	Prostemmatinae (Phorticini)							1								1			
Cimicomorpha	Nabidae	Prostemmatinae (Prostemmatini)							3								4			
Cimicomorpha	**Polyctenidae**											**1**								
Cimicomorpha	**Reduviidae**	**12 subfamilies/11 tribes**		**2**	**1**		**1**		**74**	**1**	**1**		**2**			**1**	**57**	**5**		
Cimicomorpha	Reduviidae	Ectrichodiinae (Ectrichodiini)							2								4			
Cimicomorpha	Reduviidae	Ectrichodiinae (Tribelocephalini)							1											
Cimicomorpha	Reduviidae	Emesinae (Deliastini)							1											
Cimicomorpha	Reduviidae	Emesinae (Emesini)							4								3			
Cimicomorpha	Reduviidae	Emesinae (Leistarchini)							3											
Cimicomorpha	Reduviidae	Emesinae (Metapterini)					1		2								3	1		
Cimicomorpha	Reduviidae	Emesinae (Ploiariolini)		1	1				3							1				
Cimicomorpha	Reduviidae	Harpactorinae (Harpactorini)		1					19	1	1						20	4		
Cimicomorpha	Reduviidae	Harpactorinae (Rhaphidosomini)							3								2			
Cimicomorpha	Reduviidae	Holoptilinae											1							
Cimicomorpha	Reduviidae	Peiratinae							3								3			
Cimicomorpha	Reduviidae	Phymatinae							1				1							
Cimicomorpha	Reduviidae	Reduviinae							8								10			
Cimicomorpha	Reduviidae	Saicinae							1								1			
Cimicomorpha	Reduviidae	Salyavatinae							1								1			
Cimicomorpha	Reduviidae	Stenopodainae							3								8			
Cimicomorpha	Reduviidae	Triatominae (Rhodniini)							5								1			

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Cimicomorpha	Reduviidae	Triatominae (Triatomini)							14											
Cimicomorpha	**Thaumastocoridae**				**2**							**1**	**3**							
Cimicomorpha	Thaumastocoridae	Thaumastocorinae			2							1	1							
Cimicomorpha	Thaumastocoridae	Xylastodorinae											2							
Cimicomorpha	**Tingidae**		**2**	**8**											**3**		**14**			
Cimicomorpha	Tingidae	Cantacaderinae	1	1											2					
Cimicomorpha	Tingidae	Tinginae	1	7											1		14			
Cimicomorpha	Tingidae	Vianaidinae																		
Dipsocoromorpha	**Ceratocombidae**	**Ceratocombinae**							**1**							**1**				
Dipsocoromorpha	**Dipsocoridae**				**4**										**3**					
Dipsocoromorpha	**Schizopteridae**	**Hysperosomatinae**	**2**											**1**						
Enicocephalomorpha	**Enicocephalidae**	**Enicocephalinae (Enicocephalini)**													**2**					
Gerromorpha	**Gerridae**		**1**	**6**										**15**						
Gerromorpha	Gerridae	Gerrinae		6										6						
Gerromorpha	Gerridae	Halobatinae												1						
Gerromorpha	Gerridae	Hermatobatinae												1						
Gerromorpha	Gerridae	Ptilomerinae												1						
Gerromorpha	Gerridae	Rhagadotarsinae												1						
Gerromorpha	Gerridae	Rheumatobatinae	1																	
Gerromorpha	**Hebridae**	**Hebrinae**		**2**											**3**					
Gerromorpha	**Hydrometridae**	**Hydrometrinae**															**4**			
Gerromorpha	**Mesoveliidae**	**Mesoveliinae**	**1**														**3**			
Gerromorpha	**Veliidae**		**4**									**1**	**10**							
Gerromorpha	Veliidae	Haloveliinae										1	1							
Gerromorpha	Veliidae	Microveliinae											8							
Gerromorpha	Veliidae	Rhagoveliinae	2										1							
Gerromorpha	Veliidae	Veliinae	2																	
Leptopodomorpha	**Aepophilidae**					1														
Leptopodomorpha	**Saldidae**	**Saldinae**				**1**			**2**								**2**			
Nepomorpha	**Aphelocheiridae**					**1**									**4**					
Nepomorpha	**Belostomatidae**						**6**		**1**						**5**					
Nepomorpha	Belostomatidae	Belostomatinae					5		1						3					

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Nepomorpha	Belostomatidae	Lethocerinae					1								2					
Nepomorpha	**Corixidae**						**1**		**4**								**8**			
Nepomorpha	Corixidae	Corixinae							4								7			
Nepomorpha	Corixidae	Cymatinae					1										1			
Nepomorpha	**Gelastocoridae**			**3**											**1**					
Nepomorpha	Gelastocoridae	Gelastocorinae		2																
Nepomorpha	Gelastocoridae	Nerthinae		1											1					
Nepomorpha	**Helotrephidae**	**Helotrephinae**												**1**						
Nepomorpha	**Micronectidae**			**3**													**1**			
Nepomorpha	**Naucoridae**								**3**											
Nepomorpha	Naucoridae	Limnocorinae							1											
Nepomorpha	Naucoridae	Naucorinae							2											
Nepomorpha	**Nepidae**						**2**	**1**						**1**	**6**					
Nepomorpha	Nepidae	Nepinae					1							1	2					
Nepomorpha	Nepidae	Ranatrinae					1	1							4					
Nepomorpha	**Notonectidae**			**1**					**2**								**4**			
Nepomorpha	Notonectidae	Anisopinae															1			
Nepomorpha	Notonectidae	Notonectinae		1					2								3			
Nepomorpha	**Ochteridae**			**2**													**7**			
Nepomorpha	**Pleidae**					**1**								**3**						
Pentatomomorpha	**Acanthosomatidae**	**Acanthosomatinae**				**1**		**1**	**3**								**7**		**4**	**1**
Pentatomomorpha	**Alydidae**						**1**	**1**	**3**								**6**			
Pentatomomorpha	Alydidae	Alydinae					1		3								4			
Pentatomomorpha	Alydidae	Micrelytrinae						1									2			
Pentatomomorpha	**Aradidae**	**6 subfamilies**	**1**	**2**	**1**	**18**	**3**					**1**	**4**	**2**	**19**	**6**	**1**			
Pentatomomorpha	Aradidae	Aneurinae				3	1								5					
Pentatomomorpha	Aradidae	Aradinae				1								1	2	3	1			
Pentatomomorpha	Aradidae	Calisiinae	1													1				
Pentatomomorpha	Aradidae	Carventinae		1	1	2							1	1	3					
Pentatomomorpha	Aradidae	Mezirinae		1		12						1	3		9					
Pentatomomorpha	Aradidae	Prosympiestinae					2									2				
Pentatomomorpha	**Artheneidae**	**Artheneinae**	7														**6**			

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Pentatomomorpha	**Berytidae**	**3 subfamilies**	**6**	**5**												**1**	**6**			
Pentatomomorpha	Berytidae	Berytinae	2	5													2			
Pentatomomorpha	Berytidae	Gampsocorinae	2													1	1			
Pentatomomorpha	Berytidae	Metacanthinae	2														3			
Pentatomomorpha	**Blissidae**	**Blissinae**				**1**		**6**	**5**							**5**	**4**			
Pentatomomorpha	**Coreidae**	**2 subfamilies**						**1**	**16**								**17**			
Pentatomomorpha	Coreidae	Coreinae							16								16			
Pentatomomorpha	Coreidae	Pseudophloeinae						1									1			
Pentatomomorpha	**Cydnidae**	**7 subfamilies**							**4**					**1**	**1**		**12**			
Pentatomomorpha	Cydnidae	Cephalosteinae												1						
Pentatomomorpha	Cydnidae	Cydninae							2							1	6			
Pentatomomorpha	Cydnidae	Parastrachiinae															1			
Pentatomomorpha	Cydnidae	Sehirinae							2								4			
Pentatomomorpha	Cydnidae	Thyreocorinae															1			
Pentatomomorpha	**Cymidae**														**1**		**3**			
Pentatomomorpha	Cymidae	Cyminae													1		2			
Pentatomomorpha	Cymidae	Ontiscinae							**2**								1			
Pentatomomorpha	**Dinidoridae**								**1**								**2**			
Pentatomomorpha	Dinidoridae	Dinidorinae							1								1			
Pentatomomorpha	Dinidoridae	Megymeninae															1			
Pentatomomorpha	**Geocoridae**					**5**			**1**								**3**			
Pentatomomorpha	Geocoridae	Geocorinae				5											2			
Pentatomomorpha	Geocoridae	Henestarinae							1								1			
Pentatomomorpha	**Heterogasteridae**								**4**								**2**			
Pentatomomorpha	**Largidae**	**Physopeltinae**							**1**								**2**			
Pentatomomorpha	**Lygaeidae**			**1**					**12**								**14**			
Pentatomomorpha	Lygaeidae	Ischnorhynchinae							1								1			
Pentatomomorpha	Lygaeidae	Lygaeinae							6								6			
Pentatomomorpha	Lygaeidae	Orsillinae		1					5								6			
Pentatomomorpha	**Malcidae**	**Chaulipinae**													**1**					
Pentatomomorpha	**Ninidae**						**1**								**1**					
Pentatomomorpha	**Oxycarenidae**	**Oxycareninae**		**7**													**4**			

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Pentatomomorpha	**Pachygronthidae**					**2**			**1**								**4**			
Pentatomomorpha	Pachygronthidae	Pachygronthinae															4			
Pentatomomorpha	Pachygronthidae	Teracriinae				2			1											
Pentatomomorpha	**Pentatomidae**	**6 subfamilies/18 tribes**			**5**	**8**	**7**	**26**	**36**	**1**			**1**	**1**		**12**	**43**			
Pentatomomorpha	Pentatomidae	Asopinae					1	2	4								9			
Pentatomomorpha	Pentatomidae	Discocephalinae							13	1										
Pentatomomorpha	Pentatomidae	Edessinae				3	1		1											
Pentatomomorpha	Pentatomidae	Pentatominae (Aeliini)						1	1							1				
Pentatomomorpha	Pentatomidae	Pentatominae (Agonoscelidini)						1									2			
Pentatomomorpha	Pentatomidae	Pentatominae (Antestiini)							1							1	1			
Pentatomomorpha	Pentatomidae	Pentatominae (Cappaeini)															2			
Pentatomomorpha	Pentatomidae	Pentatominae (Carpocorini)			1	2	1	12	4								6			
Pentatomomorpha	Pentatomidae	Pentatominae (Chlorocorini)						1	5											
Pentatomomorpha	Pentatomidae	Pentatominae (Eysarcorini)					1		1							5	4			
Pentatomomorpha	Pentatomidae	Pentatominae (Halyini)						1	2							1	1			
Pentatomomorpha	Pentatomidae	Pentatominae (Menidini)															1			
Pentatomomorpha	Pentatomidae	Pentatominae (Nezarini)			1			5	1								4			
Pentatomomorpha	Pentatomidae	Pentatominae (Pentatomini)			3	2		2	1								4			
Pentatomomorpha	Pentatomidae	Pentatominae (Piezodorini)					1	1									3			
Pentatomomorpha	Pentatomidae	Pentatominae (Sciocorini)															1			
Pentatomomorpha	Pentatomidae	Pentatominae (Sephelini)															1			
Pentatomomorpha	Pentatomidae	Pentatominae (Strachiini)					1		1							3				
Pentatomomorpha	Pentatomidae	Phyllocephalinae															1			
Pentatomomorpha	Pentatomidae	Podopinae (Graphosomatini)							1								2			
Pentatomomorpha	Pentatomidae	Podopinae (Podopini)					1					1	1				2			
Pentatomomorpha	Pentatomidae	Podopinae (Tarisini)				1										1				
Pentatomomorpha	**Piesmatidae**	**Piesmatinae**	**5**																	
Pentatomomorpha	**Plataspidae**								**1**							**2**	**3**			
Pentatomomorpha	**Pyrrhocoridae**								**6**								**9**			
Pentatomomorpha	**Rhopalidae**					**4**	**1**		**5**								**7**			
Pentatomomorpha	Rhopalidae	Rhopalinae				2			3								6			
Pentatomomorpha	Rhopalidae	Serinethinae				2	1		2								1			

Infraorder	Family	Subfamily (Tribe)	The number of species with a certain number of follicles per testis									The number of species with a certain number of ovarioles per ovary								
			1	2	3	4	5	6	7	8	9	2	3	4	5	6	7	8	17	24
Pentatomomorpha	**Rhyparochromidae**	**6 tribes**		2	4		3		6								33			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Antillocorini)															2			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Drymini)		2													5			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Lethaeini)															5			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Myodochini)			4		3		1								12			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Rhyparochromini)							4								5			
Pentatomomorpha	Rhyparochromidae	Rhyparochrominae (Udeocorini)							1											
Pentatomomorpha	**Scutelleridae**								6								6			
Pentatomomorpha	Scutelleridae	Odontotarsinae							1								2			
Pentatomomorpha	Scutelleridae	Pachycorinae							1											
Pentatomomorpha	Scutelleridae	Scutellerinae							4								4			
Pentatomomorpha	**Stenocephalidae**								**1**								**1**			
Pentatomomorpha	**Termitaphididae**						**1**			**1**										
Pentatomomorpha	**Tessaratomidae**	**Natalicolinae**							**1**								**1**			
Pentatomomorpha	**Urostylididae**																4			
		Total	**43**	**141**	**77**	**25**	**42**	**43**	**294**	**12**	**1**	**5**	**11**	**36**	**50**	**28**	**367**	**12**	**4**	**1**

CIMICOMORPHA

With more than 20,000 species placed in 17 families, this highly diverse infraorder is the largest within Heteroptera (Weirauch and Schuh 2011). Members of the Cimicomorpha show a wide range of adaptations to different terrestrial habitats, highly diverse life histories and prey capture strategies, including predation and blood feeding in the Reduviidae, mostly plant feeding in the Miroidea, traumatic insemination in the Cimicoidea and Miridae, and ectoparasitism in the Cimicidae and Polyctenidae. Some cimicomorphans (Cimicidae, Triatominae in Reduviidae, and Polyctenidae) are of medical importance and hematophagous at all stages (Kerzhner 1981; Schuh and Štys 1991; Schuh and Slater 1995; Schuh 1995; Tatarnic et al. 2006; Schuh et al. 2009; Weirauch and Schuh 2011; Schuh and Weirauch 2020). Data on the number of follicles and/or ovarioles are currently available for 12 families and missing for Plokiophilidae, Velocipedidae, Pachynomidae, Curaliidae, and Medocostidae.

Anthocoridae (minute pirate bugs)

The family comprises more than 500 species with seven tribes (Péricart 1972; Schuh and Štys 1991; Péricart 1996; Jung et al. 2010; Schuh and Weirauch 2020). Data are available for the number of follicles in 29 species of 12 genera from all currently recognized tribes, although ~ 40% of studied species belong to the most species-rich tribe Anthocorini. In all but six species and in all but two (the Xylocorini and Almeidini) tribes, males have two follicles p.t. The exceptions are two of the eleven studied species of the genus *Anthocoris* Fallén, 1814 (Anthocorini) having four (*A. nemorum* (Linnaeus, 1761)) and even 5–7 (*A. bakeri* Poppius, 1913) follicles p.t. Four species, *Scoloposcelis obscurella* (Zetterstedt, 1838) (Scolopini), *Australmeida derricki* (Gross, 1954), the single studied member of Almedini, and the two studied species (subgenera *Proxylocoris* and *Arrostelus*) of the genus *Xylocoris* Dufour, 1931 in the monotypic tribe Xylocorini, have seven follicles p.t. The females of six studied species (in six genera of the Anthocorini, Almeidini, Cardiastethini, Oriini, and Xylocorini) have seven ovarioles p.o.

Cimicidae (bed bugs)

The family consists of ~ 110 species and 24 genera in six recognized subfamilies (Schuh and Štys 1991; Weirauch et al. 2019). The three studied species, all belonging to the genus *Cimex* Linnaeus, 1758 (Cimicinae), have seven follicles p.t. and seven ovarioles p.o.

Joppeicidae (joppeicid bugs)

The family contains only one species, *Joppeicus paradoxus* Putton, 1881. This relict family of non-specialized general predators feeding on small insects, has an obscure history of phylogenetic placement although sometimes regarded as related to the family Tingidae (Davis and Usinger 1970; Štys 1971). Thus, any information on this spe-

cies is of considerable interest. Males of *J. paradoxus* have two follicles p.t., whereas females (according to different authors) have five or six ovarioles p.o. Five ovarioles are rarely observed in the Cimicomorpha (Davis and Usinger 1970) and its finding in Joppeicidae matches with *Cantacader* Amyot & Serville, 1843 species from the tingid subfamily Cantacaderinae and with *Corythucha marmorata* (Uhler, 1878) from the other tingid subfamily Tinginae.

Lasiochilidae (lasiochilid bugs)

A small family of predaceous true bugs with general appearance like that of Anthocoridae and Lyctocoridae and formerly classified as a subfamily within the family Anthocoridae (Schuh and Štys 1991; Schuh and Slater 1995). In two species of the genera *Lasiochilus* Reuter, 1871 and *Plochiocorella* Poppius, 1909, males have two follicles p.t. The females of *Lasiochilus* sp. have seven ovarioles p.o.

Lyctocoridae (lyctocorid bugs)

A monotypic group of predominantly predaceous true bugs formerly classified, like the Lasiochilidae, as a subfamily within the family Anthocoridae (Schuh and Slater 1995). *Lyctocoris* (*Lyctocoris*) *campestris* (Fabricius, 1794) has two follicles p.t. and seven ovarioles p.o., and the same structure of the ovaries was found in *L. beneficus* (Hiura, 1957).

Miridae (plant bugs)

The variation of testis follicle number has been used as a potentially important character for the higher-level taxonomy and phylogeny of plant bugs by several authors including Leston (1961a, b), Akingbohungbe (1983), Grozeva and Simov (2008). In total, data on 259 species, less than 3% of the entire plant bug diversity, are currently available. Eight subfamilies and 39 tribes are generally recognized within Miridae (Cassis and Schuh 2012), and data on testis follicle numbers for many of these taxa are clearly insufficient due to sampling bias. Specifically, data on Psallopinae, Austromirini of Orthotylinae, Auricillocorini of Phylinae, three of six Deraeocorinae tribes, and four of six Mirinae tribes are lacking. Only a handful of species have been studied in the subfamilies Isometopinae (one) and Cylapinae (two), the deraeocorine tribe Hyaliodini (two), the phyline tribe Hallodapini (two), orthotyline tribes Coridromiini (one), and Nichomachini (one). However, available data for better studied taxa show a stable pattern of testis follicle numbers at the tribal and sometimes also subfamily levels. The modal numbers are briefly outlined below for each sufficiently studied subfamily.

Bryocorinae

In Dicyphini, a sister clade to the remaining bryocorines (Konstantinov et al. 2018), the presence of a single follicle p.t. was documented for all 21 examined species from four gen-

era. The same appears to be true for the monotypic tribe Felisacini (two species examined). In two Dicyphini species, *Tupiocoris rhododendri* (Dolling, 1972) and *Dicyphus* (*Brachyceroea*) *annulatus* (Wolff, 1804), two follicles p.t. were found. The modal number of one was observed in the small tribe Bryocorini although Akingbohungbe (1983) documented two and two or three ("2-3") follicles for *Monalocoris filicis* (Linnaeus, 1758) and *M. americanus* Wagner & Slater, 1952, respectively. Seven examined species of Monaloniini and the only examined Eccritotarsini species *Stenopterocoris laticeps* China, 1944 have either one or three follicles p.t. Females of the permanently parthenogenetic species *Campyloneura virgula* (Herrich-Schaeffer, 1835) (Eccritotarsini) were found to have seven ovarioles p.o.

Orthotylinae

Forty-three examined species of the largest tribe Orthotylini have two follicles p.t. Only *Cyrthorhinus caricis* (Fallén, 1807) is an exception displaying testes with a single follicle each (Leston 1961a). In contrast, the tribe Halticini (eight species examined) shows no uniform pattern with a follicle number ranging from one to three.

Phylinae

Almost all species (28) of the large and diverse tribe Phylini have remarkably stable follicle number of three. Alternative structural variants found in several species, viz., *Oncotylus viridiflavus* (Goeze, 1778) (four-five), *Platyscytus decempunctatus* (Carvalho, 1945) (four to six), and *Phylus melanocephalus* (Linnaeus, 1767) (two or three in different testes of the only studied male) may be treated as isolated cases of specialization (Akingbohungbe 1983). The modal number for the tribe Pilophorini is also three, found in *Lasiolabops obscurus* Poppius, 1914 and three species from the genus *Pilophorus* Hahn, 1926 (the fourth studied *Pilophorus* species, *P. cinnamopterus* (Kirschbaum, 1856) has two follicles p.t.). The same pattern applies for the tribes Cremnorrhini (with one exception of *Orectoderus obliquus* Uhler, 1876) and Nasocorini. The tribes Hallodapini and Semiini remain insufficiently studied, but also follow the pattern of three, as evidenced by the currently available data.

Deraeocorinae

Data on this subfamily are scarce and most examined deraeocorine species (17 of 19) belong to the tribe Deraeocorini. The testis follicle number ranges from one (*Zacheila* Odhiambo, 1961, *Fingulus* Distant, 1904, and *Fingulus libbyi* Akingbohungbe, 1981) to eight (most examined species of the subgenus *Deraeocoris* Kirschbaum, 1856) and no apparent pattern for this tribe could be established at this point.

Mirinae

Being the best studied plant bug tribe (73 species examined), Mirini unequivocally have seven testis follicles (in 66 species). The exceptions are very few and include

Garganus fusiformis (Say, 1832) (two), *Capsodes gothicus* (Linnaeus, 1758) (six), *Neurocolpus jessiae* Knight, 1934 (eight), and *Poecilocapsus lineatus* (Fabricius, 1798) (eight). Noteworthy, in three species (*Adelphocoris lineolatus* (Goeze, 1778), *Leptopterna dolabrata* (Linnaeus, 1758), *Stenotus binotatus* (Fabricius, 1794)) testis follicle number varies from seven to eight in different specimens or even in a single specimen of the same species. Stenodemini, the second well examined tribe (18 species), which forms a sister clade to all other tribes of the family (Schwartz 2008), also have the modal number of seven (in seven species). However, the tribe demonstrates exceptionally high diversity of testis follicle numbers, ranging from one (*Mimoceps insignis* Uhler, 1890) to eight (*Leptopterna* spp.). Various authors documented contrastingly different numbers (3–7) for different species of the genus *Stenodema* Laporte, 1832.

Data on the number of ovarioles are available for a total of 48 species and 17 genera from the subfamilies Bryocorinae, Cylapinae, Deraeocorinae, Mirinae, Orthotylinae, Isometopinae, and Phylinae. Most species have seven ovarioles p.o. (found in 38 species, 24 genera, all subfamilies). Other numbers, including eight (in seven species, five genera), four (in one species), three (in one species), or 5–7 (in one species), occur sporadically in different subfamilies that have a modal number of seven.

Nabidae (damsel bugs)

A relatively small family of predaceous true bugs with more than 30 genera and ca. 400 species distributed in two subfamilies, Prostemmatinae (two tribes, each with only two genera) and Nabinae (four tribes) (Schuh and Štys 1991; Kerzhner 1996; Henry 2009). In Prostemmatinae, the four studied species representing the tribes Prostemmatini and Phorticini have seven follicles p.t. In the Nabinae, all ten species studied in the tribe Nabini (genera *Nabis* Latreille, 1802 and *Himacerus* Wolff, 1811) also have seven testis follicles. Available data suggest a remarkably stable follicle number of seven in these subfamilies. The only exception presently known in both Nabinae and Nabidae is *Arachnocoris trinitatis* Bergroth, 1916 (tribe Arachnocorini) which has three follicles p.t. but seven ovarioles p.o. All other studied species (16) from both subfamilies share the same pattern of seven ovarioles.

Polyctenidae (bat bugs)

The family currently comprises 32 species belonging to five genera and two subfamilies, Polycteninae and Hesperocteninae (Schuh and Weirauch 2020; Szentiványi et al. 2022). The females of the only studied species, *Hesperoctenes fumarius* (Westwood, 1874), have ovaries with two ovarioles each.

Reduviidae (assassin bugs)

With approximately 7000 species, 900 genera, and 25 subfamilies, Reduviidae are the second largest family of true bugs (Henry 2009; Hwang and Weirauch 2012; Weirauch

et al. 2014). Data on the number of follicles and/or ovarioles are available for 111 species, 72 genera and 18 subfamilies. In most species, testes are composed of seven follicles each with a few exceptions. Particularly, three of the 16 studied Emesinae species differ from that pattern. The number of follicles in *Nesidiolestes roberti* Wygodzinsky, 1966 (Emesinae, Ploiariolini) is described as "fewer than 7"; however, a figure in the original paper (Wygodzinsky 1966: fig. 11J) shows a testis with three follicles. Males of *Saicella usingeri* Wygodzinsky, 1966 (Ploiariolini) and *Bobba villiersi* Wygodzinsky, 1966 (Metapterini) were reported to have two and five follicles p.t., respectively. Within Harpactorinae (28 species studied), unusual testis follicle numbers were reported for *Polididus armatissimus* Stål, 1859 with nine follicles p.t., *Nagusta* sp. (eight), and *Repipta taurus* (Fabricius, 1803) for which two follicles p.t. were tentatively given. In *P. armatissimus*, the structure of the testis was shown to be complex: the follicles form two groups, one consisting of seven long and wide follicles and the other consisting of two smaller follicles (Gapon et al. 2021).

The testis comprising seven follicles are suggested to be an ancestral trait for the Reduviidae (Gapon et al. 2021). This testis structure has been described for *Lisarda vandenplasi* Schouteden, 1931 (Salyavatinae), eight species of the subfamily Reduviinae, 19 species of the Harpactorinae as well as for *Phymata* sp. from the Phymatinae complex, a sister group to the remaining "higher" reduviids. The number of ovarioles p.o. is seven in most species; however, some species have six (one species), three (two species), or eight (five species) ovarioles p.o. The available data suggest, thus, a high level of family stability in terms of both traits.

Thaumastocoridae (palm bugs)

The family comprises more than 30 species and six genera in two subfamilies, the Thaumastocorinae (21 species) and the Xylastodorinae (10 species) including nine recent and one described from the Dominican amber (Cassis et al. 1999; Schuh and Weirauch 2020). Data are available for four species and three genera of both subfamilies. Two species studied in the genus *Thaumastocoris* Kirkaldy, 1908 are similar in the number of follicles (two p.t.), but differ in the number of ovarioles p.o., which is three in *T. australicus* Kirkaldy, 1908 and two in *T. peregrinus* Carpintero & Dellapé, 2006. In Xylastodorinae, two species studied in the genera *Discocoris* Kormilev, 1955 and *Proxylastodoris* Heiss & Popov, 2002 are similar in having three ovarioles p.o.

Tingidae (lace bugs)

This family of herbivorous true bugs comprises ~ 2600 described species in more than 318 genera that are classified into the large subfamily Tinginae (~ 2500 species in 300 genera) and two smaller subfamilies, Cantacaderinae and Vianadinae (Golub et al. 2022). Data on follicle and/or ovariole numbers are available for a total of 25 species (12 genera) belonging to the Tinginae (21 species), Cantacaderinae (three), and Vianadinae (one). Within the Cantacaderinae, *Cantacader quadricornis* (Lepeletier &

Serville, 1828) and *C. quinquecostatus* (Fieber, 1844) were shown to have one and two follicles p.t., respectively. In the last of these species, females have ovaries with five ovarioles each, and the same structure of the ovaries is characteristic of *C. lethierryi* Scott, 1874. All studied species of the Tinginae (21 in ten genera) share consistent testis composition, with two follicles p.t. Fourteen species (ten genera) studied in terms of the ovaries have seven ovarioles; however, *Corythucha marmorata* (Uhler, 1878) has five ovarioles p.o. The only studied species from the subfamily Vianaidinae, *Anommatocoris coleopteratus* (Kormilev, 1955), has testes with a "bilobed follicle" each (Drake and Davis 1960). We are inclined to assume that this species actually has two follicles p.t.

Concluding remarks

In studied Cimicomorpha species, males may have 1–9 follicles p.t., and females may have 2–8 ovarioles p.o. Available data for the taxa where there are more data show a stable pattern of the number of follicles at different taxonomic levels. For example, seven follicles p.t. is the modal state in the families Reduviidae and Nabidae, in the tribes Mirini and Stenodemini (Miridae), and in the genus *Cimex* (Cimicidae); two follicles p.t. is the modal state in the family Anthocoridae, the subfamily Orthotylinae (Miridae) and the subfamily Tinginae (Tingidae); one follicle p.t. is the modal state in the tribe Dicyphini (Miridae). Data are scarcer on the ovariole numbers; however, in general, a pattern of seven ovarioles p.o. clearly predominates.

DIPSOCOROMORPHA

The small infraorder Dipsocoromorpha or minute litter bugs comprises ~ 430 species from 70 genera that are classified into six morphologically distinct families (Knyshov et al. 2021). Data on the number of follicles and/or ovarioles are currently available for the families Dipsocoridae, Ceratocombidae, and Schizopteridae.

Ceratocombidae (litter bugs)

This small cosmopolitan family, historically treated as a subfamily of the Dipsocoridae and raised to family level by Štys (1970), comprises eight genera and ~ 50 species in two subfamilies (Slater 1982; Štys 1995b; Henry 2009). In Ceratocombinae, *Ceratocombus* (*Ceratocombus*) *coleoptratus* (Zetterstedt, 1819) displays seven follicles p.t., and *C.* (*Xylonannus*) sp. has six ovarioles p.o.

Dipsocoridae (jumping ground bugs)

This cosmopolitan family was recently redefined to contain three genera and ca.30 species with many more awaiting descriptions (Schuh and Weirauch 2020). Data on testis and/or ovary structure are available for seven species representing all three genera. In each species studied in genera *Cryptostemma* Herrich-Schaeffer, 1835 (two species),

Alpagut Kıyak, 1995 (one), and *Pachycoleus* Fieber, 1860 (one), males have three follicles p.t. Females have five ovarioles p.o. in three studied *Cryptostemma* species while three ovarioles p.o. in *Pachycoleus pusillimus* (J. Sahlberg, 1870).

Schizopteridae (jumping soil bugs)

This family, which is the largest family of the infraorder, comprises approximately 355 species, 56 genera, and two subfamilies (Wygodzinsky 1955; Weirauch et al. 2018). Data are available for three representatives of the subfamily Hypselosomatinae. Males of *Hypselosoma hickmani* Wygodzinsky, 1959 and *Pateena polymitarior* Hill, 1980 have one follicle p.t., and females of *Hypselosoma* sp. have four ovarioles p.o.

Concluding remarks

In general, data are available for 12 species (seven genera), which is only 2.8% of the global diversity of the infraorder. Males of Dipsocoromorpha may have seven, three or one follicle p.t., the number three being characteristic of Dipsocoridae and the number one for Schizopteridae. Females may have four, five or six ovarioles p.o. It is worth noting the stability of the number of ovarioles in the genus *Cryptostemma* (three p.o.).

ENICOCEPHALOMORPHA

Unique-headed bugs comprise only two small families, Aenictopecheidae (~ 20 described species, 11 genera and four subfamilies) and Enicocephalidae (~ 300 described species, 47 genera and five subfamilies) (Štys 1995a, 2002). Enicocephalomorpha have a checkered history of phylogenetic placement and were considered as a sister group to Dipsocoromorpha (Popov 1971), a sister group to all other Heteroptera (Štys and Kerzhner 1975; Wheeler et al. 1993; Xie et al. 2008), or rendered within a clade uniting Dipsocoromorpha and Gerromorpha (Johnson et al. 2018; Weirauch et al. 2019). Data on the structure of testes for aenictopecheids and enicocephalids are lacking. However, Štys and Baňař (2008) provided a drawing of the fusiform testis in the male of *Xenicocephalus josifovi* Štys & Baňař, 2008 (Enicocephalidae, Enicocephalinae). Although the authors did not study the number of follicles, they described a testis as voluminous, suggesting that it consists of more than a single follicle. In two species of the Enicocephalidae, *Hoplitocoris lewisi* Distant 1903 and *Stenopirates japonicus* (Esaki, 1935) (Enicocephalinae), females have five ovarioles p.o.

GERROMORPHA

This infraorder of predatory, semiaquatic bugs, most of which live on the surface of the water or amongst floating plants, comprises more than 2100 species in 160 genera, eight families and five superfamilies (Polhemus and Polhemus 2008; Damgaard 2012). Data on the number of follicles and/or ovarioles are currently available for five families (not available for three very small families Hermatobatidae, Macroveliidae, and Paraphrynoveliidae).

Gerridae (water striders)

The family comprises at least 750 species and 71 genera in eight subfamilies and represents the second largest group of the infraorder in numbers of genera and species after the Veliidae (Schuh and Weirauch 2020). Data are available for the subfamilies Gerrinae (eight species, three genera), Halobatinae (six species, four genera), Hermatobatinae (one species), Ptilomerinae (one species), Rhagadotarsinae (two species, two genera), and Rheumatobatinae (one species). The number of follicles p.t. is two in all species of the Gerrinae, while males of *Rheumatobates crassifemur crassifemur* Esaki, 1926 (Rheumatobatinae) have one follicle p.t. Available data on the number of ovarioles demonstrate a highly stable pattern of four for all taxa (15 species, ten genera, five subfamilies without Rheumatobatinae for which there is no information).

Hebridae (velvet water bugs)

The family comprises 220 species and eight genera in two subfamilies (Andersen 1982; Schuh and Weirauch 2020). Data are available for the subfamily Hebrinae only, in which both studied species, *Hebrus* (*Hebrusella*) *ruficeps* Thomson, 1871 and *H.* (*Hebrus*) *pusillus* (Fallén, 1807), have two follicles p.t. These species and additionally *H.* (*Hebrus*) *nipponicus* Horváth, 1929 have five ovarioles p.o.

Hydrometridae (water measurers)

The family comprises at least 126 species and seven genera in three subfamilies (Andersen 1982). According to Pendergrast (1956), males of *Hydrometra stagnorum* (Linnaeus, 1758) (Hydrometrinae) have long and fusiform testes, each with supposedly one follicle. Females have seven ovarioles p.o. in each of the four studied species of the genus *Hydrometra* Latreille, 1797.

Mesoveliidae (pond treaders)

The family comprises ~ 50 species and 12 genera in two subfamilies and is considered a sister group to all other families of the infraorder (Schuh and Weirauch 2020). In the subfamily Mesoveliinae, *Mesovelia furcata* Mulsant & Rey, 1852 has one follicle p.t. and seven ovarioles p.o. Two more species of this genus were reported to have the same structure of the ovaries.

Veliidae (riffle bugs)

The family comprises more than 970 species and 60 genera in six subfamilies and thus represents the largest family of the infraorder (Andersen 1982). Data are available for the subfamilies Haloveliinae (two species, two genera), Microveliinae (eight species, three genera), Rhagoveliinae (two species, two genera), and Veliinae (two species, two

genera). All four riffle bug species studied in relation to the structure of the testes, two in the genus *Rhagovelia* Mayr, 1865 (Rhagoveliinae) and two others in the genus *Velia* Latreille, 1804 (Veliinae), have one follicle p.t. The number of ovarioles is also stable and equal to four in all studied species of the Microveliinae and in *Strongylovelia formosa* Esaki, 1924 from the Haloveliinae, although another species of this subfamily, *Halovelia septentrionalis* Esaki, 1924, has two ovarioles p.o.

Concluding remarks

In 43 studied species (in 21 genera) of the infraorder Gerromorpha, males may have one or two follicles p.t., and females may have two, four, five, or seven ovarioles p.o. Available data for the taxa in which more data is available demonstrate a stable pattern of the follicle number (e.g., two in Gerridae and one in Veliidae) or of the ovariole number (e.g., four in Gerridae and Veliidae, and seven in Hydrometridae).

LEPTOPODOMORPHA

The infraorder (shore bugs) comprises ca. 380 species in 42 genera and four extant families, including two larger Saldidae and Leptopodidae, both of worldwide distribution, and two rare and highly endemic families, the Omaniidae with four species in two genera, and monotypic Aepophilidae (Schuh and Polhemus 1980; Schuh et al. 1987; Schuh and Slater 1995; Polhemus and Polhemus 2012; Larivière and Larochelle 2019).

Aepophilidae (marine bugs)

This enigmatic taxon encompasses a single species, *Aepophilus bonnairei* Signoret, 1879 that has seven follicles p.t. in males.

Saldidae (shore bugs)

The family comprises ~ 335 species in 29 genera. Two studied species of the genus *Saldula* Van Duzee, 1914, *S. arenicola* (Scholtz, 1847) and *S. saltatoria* (Linnaeus, 1758), have seven follicles p.t., whereas *Halosalda lateralis* (Fallén, 1807) has four follicles p.t. Seven ovarioles p.o. were found in *Macrosaldula scotica* (Curtis, 1833) and *Saldula arenicola* (Scholtz, 1847).

Concluding remarks

In five studied species of Leptopodomorpha (four genera, two families), males have seven or four follicles p.t. in four and one species, respectively. Note that the first number occurs in both explored families, and the same number of ovarioles p.o. is found in females of two studied species in two genera of shore bugs.

NEPOMORPHA

The infraorder Nepomorpha or water bugs is one of the most specialized groups of heteropterans, with most of its species spending the entire life cycle within the water. It comprises more than 2300 species arranged in 140 genera and 13 families (Polhemus and Polhemus 2008; Ribeiro et al. 2018; Ye et al. 2019). Data on the number of follicles and/or ovarioles are currently available for all but two (Diaprepocoridae and Potamocoridae) families.

Aphelocheiridae (benthic water bugs)

The family comprises at least 78 species in the only genus *Aphelocheirus* Westwood, 1833 (Polhemus and Polhemus 2008). In *A. aestivalis* (Fabricius, 1794), males have four follicles p.t. and five ovarioles p.o., and the same structure of the ovaries was found in three more species of the genus.

Belostomatidae (giant water bugs)

The family comprises ca. 160 species and 11 genera in three subfamilies (Perez-Goodwyn 2006). Presently, data on testis and/or ovary structure are available for eight species in four genera of the subfamily Belostomatinae (*Belostoma* Latreille 1807, *Diplonychus* Laporte, 1833, *Appasus* Amyot & Serville, 1843, and *Adebus* Stål, 1862), and three species of the subfamily Lethocerinae (genus *Lethocerus* Mayr, 1853). All five studied *Belostoma* species have five follicles p.t., whereas the only studied *Diplonychus* species, *D. rusticus* (Fabricius, 1781), has seven follicles p.t. In *Lethocerus indicus* (Lepeletier & Serville, 1825), testes consist of five follicles each, and in *L. patruelis* (Stål, 1854), the number of follicles p.t. is questionable (five or four). Females of the four studied species in the genera *Belostoma* (one species), *Diplonychus* (one), *Adebus* (one), and *Lethocerus* (one) have five ovarioles p.o.

Corixidae (water boatmen)

The family comprises 607 species and 35 genera in four subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data on testis and/or ovary structure are available for seven species of the subfamily Corixinae and the only representative of the subfamily Cymatinae, *Cymatia coleoptrata* (Fabricius, 1777). All studied Corixinae species from the genera *Sigara* Fabricius, 1775 (two species), *Cenocorixa* Hungerford, 1948 (one) and *Corixa* Geoffroy, 1762 (one) have seven follicles p.t., whereas male *C. coleoptrata* has five follicles p.t. The ovaries in all studied species (eight species, five genera, both subfamilies) consist of seven ovarioles each.

Gelastocoridae (toad bugs)

The family comprises at least 111 species and three genera from two subfamilies and belong to the secondarily terrestrial superfamily Ochteroidea (Hebsgaard et al. 2004).

Data are available for four species. Two species in the genus *Gelastocoris* Kirkaldy, 1897 (Gelastocorinae) have two follicles p.t., and the same testis structure is typical for *Nerthra terrestris* (Kevan, 1948) from the subfamily Nerthrinae. Females of *Nerthra macrothorax* (Montrouzier, 1855) have five ovarioles p.o.

Helotrephidae (backswimmers)

The family comprises more than 170 species (Papáček and Zettel 2005) and is considered as a sister group to the Pleidae (Chen et al. 2005). *Helotrephes formosanus* Esaki & Miyamoto, 1943, the only explored species of the family, has four ovarioles p.o., that is the same number that have females in the Pleidae (see below).

Micronectidae (pygmy boatmen)

The family comprises 150 species and five genera in two subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data are available for three species of *Micronecta* Kirkaldy, 1897 (Micronectinae), in which males were reported to have two follicles p.t.

Naucoridae (creeping water bugs)

The family comprises ~ 420 species and 43 genera in six subfamilies (Sites 2022). All three species studied in the genera *Limnocoris* Stål, 1860 (Limnocorinae), *Pelocoris* Stål, 1876, and *Ilyocoris* Stål, 1861 (Naucorinae) have seven follicles p.t. Various authors reported different numbers of ovarioles (seven or five) p.o. for *Ilyocoris cimicoides* (Linnaeus, 1758).

Nepidae (water scorpions)

The family comprises 268 species and 15 genera from two subfamilies (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data on the follicle number are available for three species in two genera, *Ranatra* Fabricius, 1790 (Ranatrinae) and *Nepa* Linnaeus, 1758 (Nepinae). *Nepa cinerea* Linnaeus, 1758 have five follicles p.t., whereas males of *R. fusca* Palisot de Beauvois, 1820 and *R. linearis* (Linnaeus, 1758) have six and five follicles p.t., respectively. Among seven species with known structure of ovaries, all four *Ranatra* spp. share five ovarioles p.o., whereas two species of the genus *Laccotrephes* Stål, 1866 (Nepinae), *L. japonensis* Scott, 1874 and *L. maculatus* (Fabricius, 1775), have five and four ovarioles p.o., respectively.

Notonectidae (backswimmers)

The family comprises ~ 400 species and 11 genera in two subfamilies, Notonectinae and Anisopinae (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Data are available for four species only. In Notonectinae, *Notonecta glauca* Linnaeus, 1758 and

N. maculata Fabricius, 1794 have seven follicles p.t., whereas *Martarega bentoi* Truxal, 1949, the only studied species in the Anisopinae, has two follicles p.t. Ovaries (examined in three species of *Notonecta* Linnaeus, 1758) consist of seven ovarioles each.

Ochteridae (velvety shore bugs)

The family comprises at least 68 species and belongs to the lineage of the aquatic Nepomorpha, which returned to a terrestrial way of life. Most authors consider Ochteridae as a sister group to the Gelastocoridae (e.g., Hebsgaard et al. 2004; Hua et al. 2009). The only examined species of the family, *Ochterus marginatus marginatus* (Latreille, 1804), shares two follicles p.t. with studied gelastocorids (see above), but has seven ovarioles p.o.

Pleidae (pygmy backswimmers)

The family comprises ~ 40 species in three genera (Polhemus and Polhemus 2008; Schuh and Weirauch 2020). Males of *Plea minutissima* Leach, 1817 have four follicles p.t., and females have four ovarioles p.o. The same structure of the ovaries is characteristic of *Paraplea indistinguenda* (Matsumura, 1905) and *P. japonica* (Horváth, 1904).

Concluding remarks

In studied Nepomorpha species, males may have testes with different numbers of follicles (two to seven, except three), and females have ovaries with different numbers of ovarioles (four, five or seven). The numbers seven, five and two are most common, being found in 32%, 29% and 26% of studied species, respectively. In females, ovaries with five and seven ovarioles occur in 52% and 45% of studied species, respectively. Available data for relatively more fully studied taxa show a stable pattern of the follicle number at the generic level, e.g., five in *Belostoma* and two in *Micronecta* Kirkaldy, 1897, as well as at the subfamily level (seven in Corixinae), and it seems also at the family level (two in Gelastocoridae and Micronectidae). The ovariole numbers appear to show a stable pattern in some families (seven in Corixidae and Notonectidae, five in Aphelocheiridae, and four in Pleidae). However, only 50 species (in 25 genera) have been studied in the infraorder in general, i.e., ~ 2% of the global diversity of the group, which is, of course, too small to draw any conclusions.

PENTATOMOMORPHA

With nearly 15 000 extant species, this worldwide distributed group is the second largest infraorder of true bugs, with 40 currently recognized families arranged in six superfamilies viz., Aradoidea, Idiostoloidea, Coreoidea, Lygaeoidea, Pyrrhocoroidea, and Pentatomoidea (Weirauch et al. 2019; Schuh and Weirauch 2020). The majority

of pentatomorphan insects are terrestrial and phytophagous, but some of them are predaceous (Schuh and Slater 1995; Weirauch and Schuh 2011; Liu et al. 2019). Data on the number of follicles and/or ovarioles are currently available for 433 species (2.4%), 274 genera and 28 families (70%) in all superfamilies except Idiostoloidea, a small and poorly studied group containing six species only.

ARADOIDEA

Aradidae (flat bugs)

The family comprises approximately 1900 species, more than 230 genera, and eight subfamilies (Heiss 2001). Data on the number of follicles and/or ovarioles are available for 41 species, 17 genera and six subfamilies (unavailable for Isoderminae and Chinamyersiinae).

Prosympiestinae. In two studied species of the genus *Prosympiestus* Bergroth, 1894, males have six follicles p.t. and females have six ovarioles p.o.

Carventinae. Data are available for the genera *Carventus* Stål, 1865 (two species), *Euricoris* Kormilev, 1957 (two species), and *Paracarventus* Kormilev, 1964 (one species). Both testes and ovaries have the same range of numbers, three, four, or five, in each case the numbers of follicles and ovarioles coinciding in the same species.

Calisiinae. In *Calisius hackeri* Kormilev, 1958, males have two follicles p.t. and females have six ovarioles p.o.

Aneurinae. Data are available for the genera *Aneurus* Curtis, 1825 (six species) and *Paraneurus* Jacobs 1986 (one species). Both genera are characterized by a stable pattern of five follicles p.t. and five ovarioles p.o., with the only exception of *A.* (*Aneurus*) *laevis* (Fabricius, 1775) having six follicles p.t. For *Aneurus* (*Aneurodes*) *avenius* (Dufour, 1833) four and five ovarioles are reported by different authors.

COREOIDEA

Coreidae (leaf-footed bugs)

The family comprises more than 2570 extant species described in four subfamilies and 37 tribes (Coreoidea SF Team 2019). Data are available for the subfamilies Coreinae and Pseudophloeinae. The first is distinguished by the high stability of the structure of the testes and ovaries having seven follicles p.t. in all 16 studied species in 14 genera and the same number of ovarioles p.o. in all 16 studied species in nine genera. In the second subfamily, *Coriomeris hirticornis* (Fabricius, 1794) also has seven ovarioles p.o., although *Ceraleptus lividus* Stein, 1858 has six follicles p.t.

Rhopalidae (scentless plant bugs)

The family comprises more than 200 species in 30 genera and two subfamilies, the Rhopalinae and the Serinethinae (Schuh and Weirauch 2020). Data are available for 11 species and seven genera of both subfamilies. A testis may consist of four, five, or seven follicles, but the number of seven prevails (found in seven species, six genera, both subfamilies).

Stenocephalidae (spurgebugs)

In the sole genus of the family, *Dicranocephalus* Hope, 1831, one species has seven follicles p.t. and seven ovarioles p.o. (*D. agilis* (Scopoli, 1763)), whereas another species (*D. albipes* (Fabricius, 1781)) has five follicles p.t.

LYGAEOIDEA

Artheneidae

This group contains slightly more than 20 species arranged in seven genera and three subfamilies, with most species belonging to Artheneinae, while Dilompinae and Nothochrominae remain monotypic (Henry 1997a; Schuh and Weirauch 2020). The reproductive system was studied in seven species belonging to three genera or one-third of the described diversity of Artheneinae. A uniform pattern of two follicles p.t. and seven ovarioles p.o. was revealed in all cases.

Berytidae (stilt bugs)

This worldwide family comprises ~ 37 genera and 174 species in three subfamilies (Henry 1997b, c; Henry et al. 2015). Data are available for ~ 19% and 8% of genera and species, respectively, belonging to all subfamilies, Berytinae (seven species, three genera), Gampsocorinae (three species, one genus), and Metacanthinae (four species, three genera). There is one follicle p.t. in the two latter subfamilies and two, but sometimes one, in the Berytinae. The number of ovarioles is seven p.o. in all but one species studied. These species represent all three subfamilies and the only exception is *Gampsocoris viridiventris* (Matsumura, 1907) (Gampsocorinae), which has six ovarioles p.o. although another species of the same genus, *G. culicinus* Seidenstücker, 1948, has seven.

Blissidae

This family of strongly flattened and sap sucking lygeoids has a worldwide distribution and currently contains more than 400 species belonging to ca. 50 genera (Schuh and Weirauch 2020). No suprageneric classification was ever proposed for this group,

and the reproductive system was studied in 14 species from six genera. Of these, the most frequent number of follicles p.t. equals six, documented in all studied *Blissus* Burmeister, 1835 spp., *Macropes raja* Distant, 1909 and *Iphicrates spinicaput* (Scott, 1874). However, seven follicles p.t. were also frequently observed across some studied taxa, e.g., *Ischnodemus* spp., *Macropes obnubilus* (Distant, 1883), *Iphicrates spathus* Slater, 1961, and *Heinsius explicatus* Distant, 1901, and four follicles were documented for *Cavelerius saccharivorus* (Okajima, 1922). The number of ovarioles is either seven or six and appears to correspond to the number of follicles in males of a given species. *Cavelerius saccharivorus* (Okajima, 1922) forms the only exception, having six ovarioles but four follicles.

Cymidae

This group contains at least 64 species in ten genera classified into two subfamilies, Cyminae and Ontiscinae (Schuh and Weirauch 2020). Despite easy accessibility for specimen collecting, data on the male reproductive system are scarce. Two species of the genus *Ontiscus* Stål, 1874 were studied so far and possess both seven follicles p.t. Seven ovarioles p.o. were documented for three species from both subfamilies, and five ovarioles p.o. were registered in *Cymus aurescens* Distant, 1883.

Geocoridae (big-eyed bugs)

This family comprises 27 genera and ~ 280 species in five subfamilies (Henry et al. 2015). In the genus *Geocoris* Fallén, 1814 (Geocorinae), males have four follicles p.t. (five species) and females have seven ovarioles p.o. (two species). Males of *Henestaris halophilus* (Burmeister, 1835) (Henestarinae) have seven follicles p.t. and females have seven ovarioles p.o.

Heterogastridae

This small family currently consists of 23 genera and at least 105 species (Schuh and Weirauch 2020), four of which were studied in regard to the structure of the testes and ovaries. All three studied species of the genus *Heterogaster* Schilling, 1829 and *Platyplax salviae* (Schilling, 1829) have seven follicles p.t., and females of two studied *Heterogaster* spp. have seven ovarioles p.o.

Lygaeidae (seed bugs)

The family comprises 107 genera and more than 970 species in three subfamilies (Henry et al. 2015). Data are available for 16 species and six genera of the subfamilies Ischnorhynchinae (two species, two genera), Lygaeinae (nine species, five genera), and Orsillinae (seven species, three genera). Except for *Paranysius fraterculus* (Burmeister, 1835) (Orsillinae) having two follicles p.t., the number of follicles and ovarioles in seed bugs equals seven (p.t. and p.o., respectively).

Malcidae

The family comprises more than 40 described species and three genera in two subfamilies (Schuh and Weirauch 2020). In the only studied species, *Chauliops fallax* Scott, 1874 (Chaulipinae), females have five ovarioles p.o.

Ninidae

Five genera and 14 species are recognized in this small pantropical group (Schuh and Weirauch 2020). Among the two species studied, males of *Ninomimus flavipes* (Matsumura, 1913) have five follicles p.t., and the females of *Ninus insignis* Stål, 1860 have five ovarioles p.o.

Oxycarenidae

This worldwide distributed family contains slightly less than 150 species from 27 genera not arranged into subfamilies or tribes (Schuh and Weirauch 2020). All studied species have two follicles p.t. (eight species from six genera) and seven ovarioles p.o. (four species from four genera).

Pachygronthidae

With more than 80 species arranged in 14 genera, this predominantly tropical and subtropical taxon clusters into two subfamilies, Pachygrontinae and Teracriinae (Slater 1955). Available data on the morphology of the reproductive system are scarce, with four (two species) and seven (one species) follicles p.t. documented for Teracriinae. Female reproductive system has only been studied in four *Pachygrontha* spp. (Pachygronthinae) resulting in seven ovarioles p.o. in each case.

Piesmatidae

This small but nonetheless worldwide distributed group contains less than 50 species arranged in six genera and two morphologically and ecologically distinct subfamilies, Piesmatinae and Psamminae (Henry 1997a; Schuh and Weirauch 2020). While the reproductive system of Psamminae has never been studied, all six species from two genera of the subfamily Piesmatinae were shown to have two follicles p.t. The ovaries have been studied in only one species, *Parapiesma quadratum* (Fieber, 1844), that has been observed to have four or six ovarioles p.o.

Rhyparochromidae (dirt-colored seed bugs)

The family comprises more than 2000 species in two subfamilies, Plinthisinae and Rhyparochrominae, the latter with 14 tribes (Henry 1997a). Data are available for 40

species and 29 genera of the Rhyparochrominae (six tribes). The number of ovarioles p.o. is seven in all studied species, whereas the number of follicles p.t. is either two (in Anthillocorini and Drymini), three or five (in different genera of Myodochini), or seven (in the single species of Myodochini, and in all studied species of Udeocorini and Rhyparochromini), seven clearly prevailing in the family.

PENTATOMOIDEA

Acanthosomatidae

The family comprises more than 50 genera and more than 280 species in three subfamilies (Schuh and Slater 1995; Henry 2009; Schuh and Weirauch 2020). Data on the testis and ovary structure are available for 15 species within five genera of the subfamily Acanthosomatinae. The number of follicles may be seven (three species, three genera), four (one species) or six (one species), and both last numbers occur in the genus *Rhopalimorpha* Dallas, 1851 (*Rh. lineolaris* Pendergrast, 1950 and *Rh. obscura* Dallas, 1851, respectively). The number of ovarioles is seven in the majority (seven) of species. The genus *Elasmucha* Stål, 1864 is of interest showing seven ovarioles in *E. graminea* (Distant, 1883) while unusually high numbers, 17 and even 24, in five other species.

Cydnidae (burrowing bugs)

The family comprises more than 1180 species in ca. 145 genera worldwide, arranged in nine subfamilies (Henry 2009). Data are available for the subfamilies Cephalosteinae, Cydninae, Parastrachiinae, Sehirinae, and Thyreocorinae. In all species studied in the subfamilies Cydninae (two species, two genera) and Sehirinae (two species, two genera), testes consist each of seven follicles. Fourteen species (13 genera, five subfamilies) were studied with respect to the ovaries, and twelve of them have seven ovarioles p.o.; however, *Stibaropus* sp. (Cephalosteinae) and *Chilocoris confusus* Horváth, 1919 (Cydninae) have four and five ovarioles p.o., respectively.

Dinidoridae

The family comprises ~ 100 species in 16 genera and two subfamilies (see Lis et al. 2012 for references). The testis and ovary of *Coridius janus* (Fabricius, 1775) (Dinidorinae) consist of seven follicles and seven ovarioles, respectively, and the same structure of the ovaries is found in *Megynemum gracilicorne* Dallas, 1851 (Megymeninae).

Pentatomidae (stink bugs)

This third largest true bug family comprises almost 5 000 species in ca. 940 genera distributed in nine subfamilies including Asopinae, Cyrtocorinae, Discocephali-

nae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae,Serbaninae, and Stirotarsinae (Rider 2006; Rider et al. 2018; Schuh and Weirauch 2020). Data on the testes and ovaries are available for all subfamilies, except Cyrtocorinae, Serbaninae, and Stirotarsinae. In total, the testis structure was studied in males of 88 species of 63 genera and five subfamilies (there is no data for Phyllocephalinae), and the structure of ovaries is studied in females of 57 species in 41 genera (Pentatominae, Asopinae, Podopinae, and Phyllocephalinae). The number of follicles varies from three to eight, but seven follicles appear to be the most frequent state being found in each subfamily and in most studied species and genera. The observed numbers of ovarioles were three, four, six, or seven and, like in the case of the number of follicles, seven ovarioles p.o. is the most common pattern found in more than two thirds of species and genera studied in this regard (43 species, 36 genera, all four subfamilies). Other numbers were observed in 14 species only. Nine of these species belong to the genera *Eysarcoris* Hahn, 1834 and *Eurydema* Laporte de Castelnau, 1833 (Pentatominae, Eysarcorini, and Strachiini respectively), for which the characteristic number is six. For some species, different authors reported different numbers for the same species, for example, six and seven for *Eysarcoris ventralis* (Westwood, 1837) and *Nezara viridula* (Linnaeus, 1758). In *Bagrada* (*Bagrada*) *hilaris* (Burmeister, 1835), different numbers of ovarioles were observed in different ovaries of the same specimen.

Pentatomids are remarkable in that their testes may possess a so-called "harlequin" lobe, in which meiosis is aberrant leading to the production of spermatids carrying numerically unbalanced chromosome complement with an abnormal and highly variable chromosome number (Schrader 1960a). Speculation on the evolutionary aspects of the harlequin lobe can be found in Schrader (1960b). To date, this specific follicle has been found mostly in the subfamilies Discocephalinae, Edessinae, and Pentatominae (Rebagliati et al. 2005).

Plataspidae

The family comprises ~ 530 species in 56 genera (Jessop 1983). The only species studied with respect to the testes, *Coptosoma* sp., has seven follicles p.t., and five species studied with respect to the ovaries have seven (three species, two genera) and six (two species, two genera) ovarioles p.o.

Scutelleridae (jewel bugs)

The family comprises ~ 80 genera and 500 described species worldwide (Tsai et al. 2011). Data are available for 11 species in nine genera of the subfamilies Odontotarsinae (three species, two genera), Pachycorinae (one species), and Scutellerinae (seven species, six genera). All species have seven follicles p.t. (six species studied) and seven ovarioles p.o. (six species studied).

Tessaratomidae

The family comprises three subfamilies, 49 genera and ~ 235 species worldwide (Rolston et al. 1993). The only studied species, *Cyclogastridea nigromarginalis* Reuter, 1884 (Natalicolinae), has seven follicles p.t. and seven ovarioles p.o.

Urostylididae

The family comprises four genera and ca. 80 species (Rider et al. 2018). No data on the male reproductive system are available at the moment. In three species of the genus *Urostylis* Westwood, 1837 and in *Urochela luteovaria* Distant, 1881, females have seven ovarioles p.o.

PYRROCOROIDEA

Largidae (bordered plant bugs)

The family comprises ~ 200 species in two subfamilies worldwide. In the subfamily Physopeltinae, *Physopelta gutta* (Burmeister, 1834) has seven follicles p.t. and seven ovarioles p.o.

Pyrrhocoridae (cotton stainers)

The family comprises more than 300 species worldwide in at least 30 genera and two subfamilies. Data are available for 11 species in four genera of the subfamily Pyrrhocorinae; all examined species have seven follicles p.t. and seven ovarioles p.o. The only exception is *Dysdercus* (*Paradysdercus*) *koenigii* (Fabricius, 1775) with a variable number of 5–7 follicles p.t.

Concluding remarks

In Pentatomomorpha species studied, males may have 3–8 follicles p.t., and females 3–7 ovarioles p.o., except the genus *Elasmucha* (Acanthosomatidae) in which a unique diversity (7–24 ovarioles p.o.) has been reported for the five studied species. The number seven is characteristic for some higher taxa studied in relation to the structure of the testes and ovaries (among the better studied families, these are Coreidae, Cydnidae, Lygaeidae, and Pentatomidae). The exception is the family Aradidae for which this number seems to not be characteristic of either the ovaries or the testes, with seven being only reported for the ovaries of *Aradus* (*Aradus*) *pictus* Baerensprung, 1859. In some families (e.g., Artheneidae, Oxycarenidae, Berytidae), the number seven is typical for the ovaries but not for the testes, which consist either of two follicles (in the first two families) or of one follicle (in the third family).

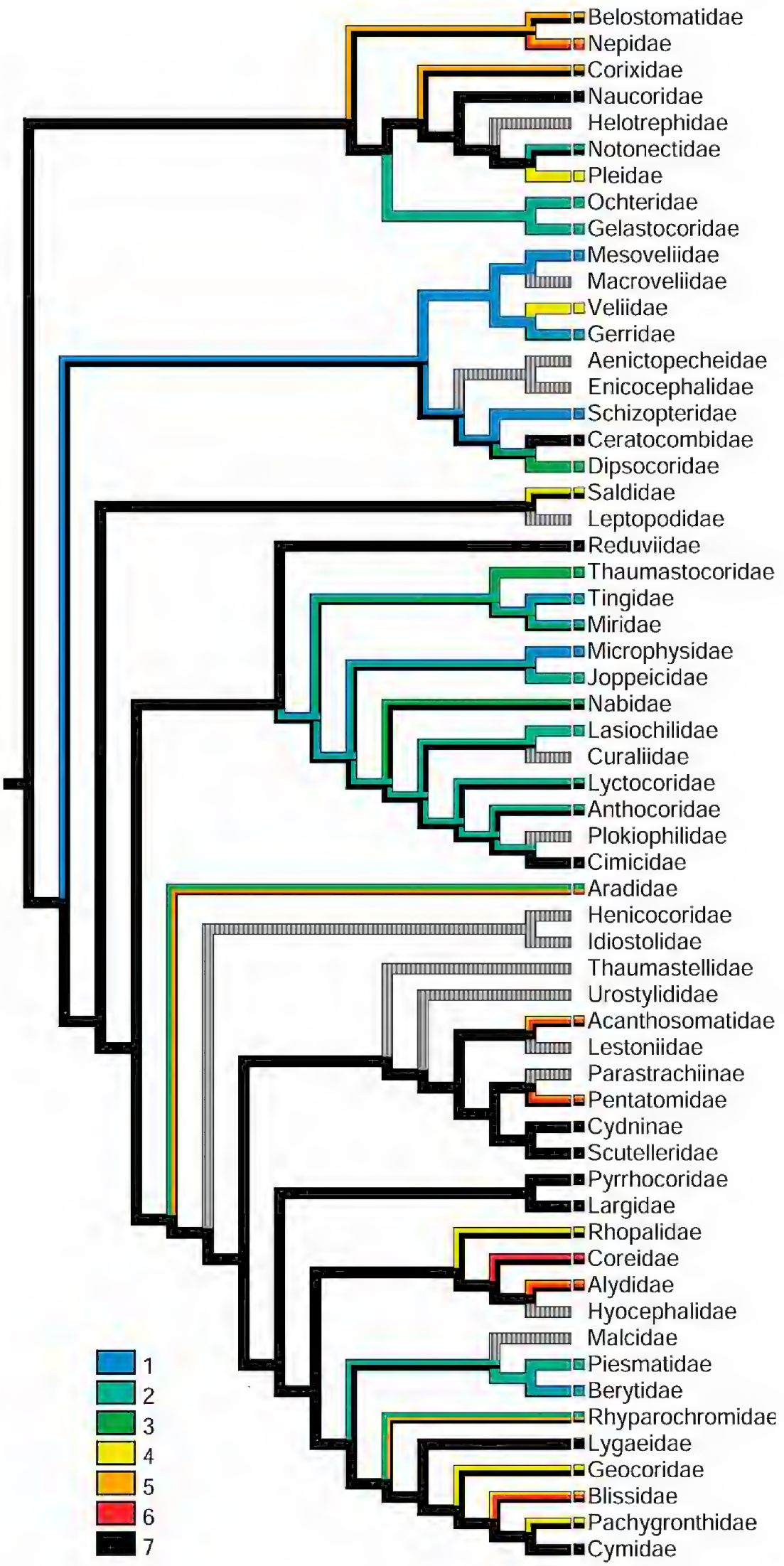

Figure 2. Testicular follicle numbers mapped on the true bug phylogeny after Weirauch et al. (2019).

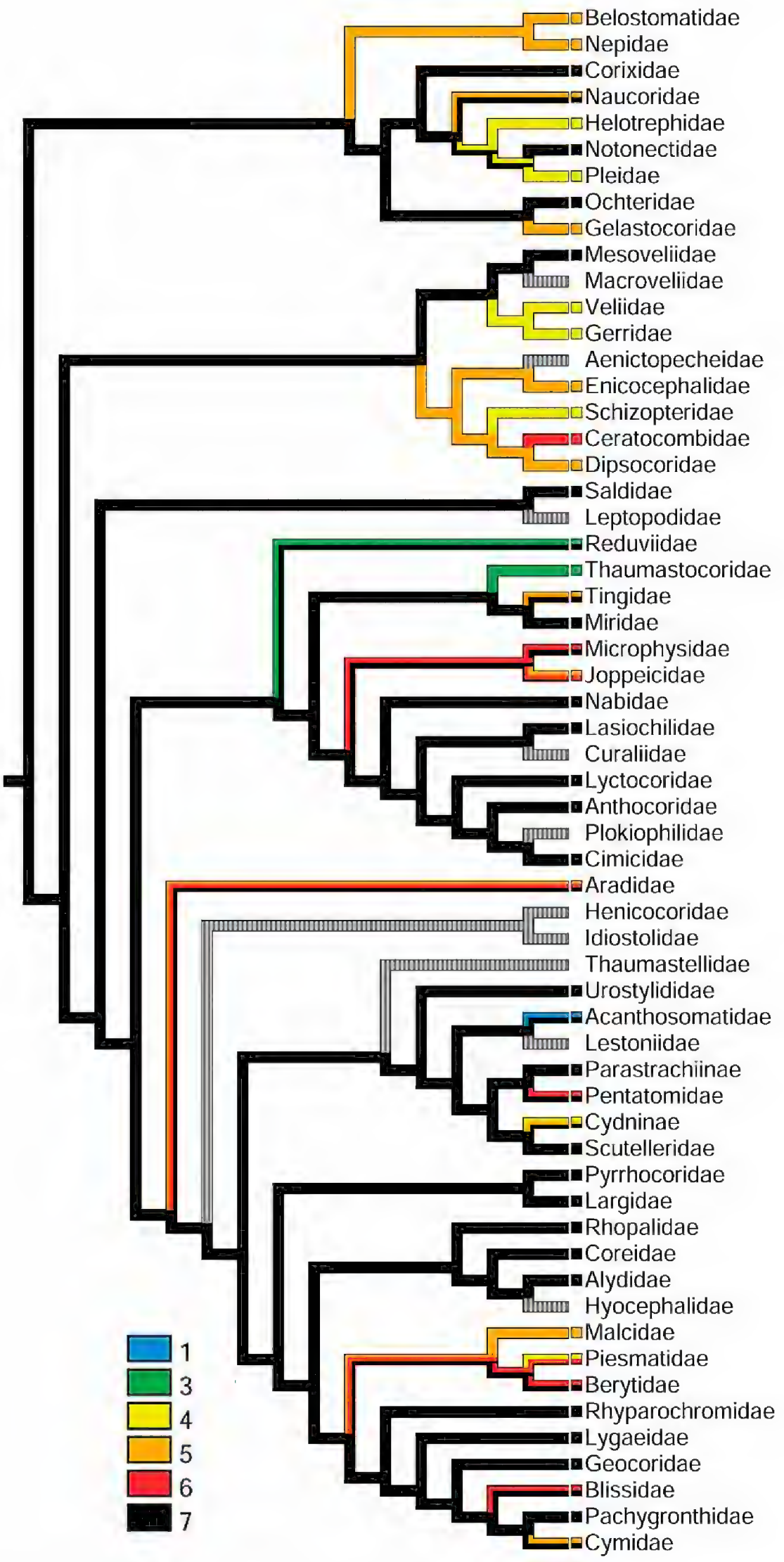

Figure 3. Ovariole numbers mapped on the true bug phylogeny after Weirauch et al. (2019).

Conclusions

In this study, we analyzed the number of follicles in testes of 705 species (420 genera, 58 families) and the number of ovarioles in ovaries of 504 species (334 genera, 61 families) across all seven major lineages of the suborder Heteroptera (Figs 2, 3, Suppl. material 1). Our comprehensive review showed that the gonads in true bugs are paired organs, and the testis and the ovary may consist of a variable number of follicles and ovarioles ranging from one to nine and from one to eight (while occasionally even to 24 in some Acanthosomatidae) respectively. Approximately 40% of species have seven follicles p.t. and ~ 68% of species have seven ovarioles p.o. Numbers exceeding this modal value are rare; the exception is eight follicles in the genus *Deraeocoris* Kirschbaum, 1855 (Miridae), in which almost half of the studied species have this number. Lower numbers, on the other hand, are quite common; moreover, sometimes they characterize taxa of high rank. In the families Miridae, Pentatomidae, and Reduviidae, for which there is relatively much data, a variety of numbers is observed. It is most pronounced in the Miridae in which data on testes and ovaries are available for 220 and 48 species, respectively. Although the number of ovarioles in most mirid species is seven, the number of follicles varies widely, from one to eight (except five), the number seven and lower numbers (1–3) occurring with almost equal frequency. Some other families, e.g., Anthocoridae, Aradidae, Belostomatidae, Berytidae, Gerridae, Oxycarenidae, and Tingidae, usually have low numbers of follicles. Noteworthy is also the family Aradidae, in which ovarioles vary in number, with numbers below the modal predominating. However, there is still very little data for all these families.

Ancestral reconstruction of testes suggests seven follicles p.t. as an ancestral state for true bugs (Fig. 2). This number was also recovered for the common ancestors of Pentatomomorpha and all its superfamilies except Aradoidea, Cimicomorpha, Leptopodomorpha, and Nepomorpha. This is consistent with the fact that seven follicles p.t. were documented in the majority of studied species across Heteroptera (Suppl. material 1; Akingbohungbe 1983). However, the common ancestor of Gerromorpha appears to have a testis with one follicle, while the parsimony reconstruction for Enicocephalomorpha and Dipsocoromorpha indicates equal probability of one or seven follicles as an ancestral state. This variation in ancestral traits is noteworthy, given the ongoing debates on the backbone phylogeny of the Heteroptera, implying Enicocephalomorpha (Wheeler et al. 1993; Xie et al. 2008), Enicocephalomorpha + Dipsocoromorpha (Wang et al. 2016), or these two infraorders + Gerromorpha (Johnson et al. 2018) as a sister group to the remaining infraorders, or Panheteroptera. In all studied species of Peloridiidae (Coleorrhyncha), which is usually considered as a sister group to Heteroptera both on morphological (Schlee 1969; Grimaldi and Engel 2005), molecular (Xie et al. 2008; Cryan and Urban 2012), and cytogenetic (Kuznetsova et al. 2015) grounds, testes also consist of a single follicle (Grozeva et al. 2014).

Reconstruction of an ancestral state for ovaries (Fig. 3) indicates a similar, but more straightforward, result, giving seven ovarioles p.o. for the entire clade, Pentatomomorpha (and all recognized superfamilies except Aradoidea), Cimicomorpha (and all included superfamilies except Microphysoidea and Reduvioidea), Leptopodomorpha, Gerromor-

pha, and Nepomorpha. The infraorders Enicocephalomorpha and Dipsocorimorpha form an exception, with five ovarioles p.o. recovered for each of them as an ancestral state.

Summing up, the number of seven appears to be an ancestral state for both testes and ovaries of true bugs. It is still retained in many lineages but may increase or decrease in separate groups. The trend towards decreasing the number of follicles and ovarioles undoubtedly prevailed in the evolution of the suborder Heteroptera in general.

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References

Adams TS (2001) Morphology of the internal reproductive system of the male and female two-spotted stink bug, *Perillus bioculatus* (F.) (Heteroptera: Pentatomidae) and the transfer of products during mating. Invertebrate Reproduction & Development 39(1): 45–53. https://doi.org/10.1080/07924259.2001.9652466

Akingbohungbe AE (1983) Variation in testis follicle number in the Miridae (Hemiptera: Heteroptera) and its relationship to the higher classification of the family. Annals of the Entomological Society of America 76(1): 37–43. https://doi.org/10.1093/aesa/76.1.37

Andersen EA (1982) The semiaquatic bugs (Hemiptera, Gerromorpha): phylogeny, adaptations, biogeography, and classification. Brill, Leiden, 455 pp.

Araújo VA, Bacca T, Dias LG (2020a) Anatomy of male and female reproductive organs of stink bugs pests (Pentatomidae: Heteroptera) from soybean and rice krops. Biota Neotropica 20(4): e20201045. https://doi.org/10.1590/1676-0611-bn-2020-1045

Araújo VA, Oliveira AS, Cortes ICH, Viteri-D J, Dias LG (2020b) Morphology of the male reproductive tract in two species of phytophagous bugs (Pentatomidae: Heteroptera). Journal of Entomology and Zoology Studies 8: 1608–1614.

Araújo VA, Bacca T, Dias LG (2021) Histology of the male reproductive tract of the assassin bug *Zelus longipes* (Heteroptera: Reduviidae). Caldasia 43(1): 39–48. https://doi.org/10.15446/caldasia.v43n1.85745 [online]

Barth R (1958) Estudos anatômicos e histológicos sobre a subfamília Triatominae (Hemiptera, Reduviidae). IX parte: Vaso deferente e mesadênias de *Triatoma infestans*. Memorias do Instituto Oswaldo Cruz 56(1): 209–238. https://doi.org/10.1590/S0074-02761958000100011 [MIOC]

Baumgartner WJ, Witherspoon W (1937) Spermatid transformation in *Anasa tristis* (De Geer). Transactions of the Kansas Academy of Science 40: 327–339. https://doi.org/10.2307/3625428

Bhargava S (1967) Morphology, musculature and innervation of the reproductive organs of *Lethocerus indicum* (Hemiptera: Belostomatidae). Journal of Kansas Entomological Society 40(1): 111–124. https://www.jstor.org/stable/25083602

Biliński SM, Ksiażkiewicz-Kapralska M, Štys P (1990) Unusual organization of the tropharium in the telotrophic ovarioles of an insect, *Saldula saltatoria*. Tissue & Cell 22(2): 213–219. https://doi.org/10.1016/0040-8166(90)90023-3

Bonhag PF, Wick JR (1953) The functional anatomy of the male and female reproductive systems of the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae). Journal of Morphology 93(2): 177–283. https://doi.org/10.1002/jmor.1050930202

Bowen RH (1922a) Notes on the occurrence of abnormal mitoses in spermatogenesis. The Biological Bulletin 43(3): 184–202[, 202-1]. https://doi.org/10.2307/1536740

Bowen RH (1922b) Studies on insect spermatogenesis. IV. The phenomenon of polymegaly in the sperm cells of the family Pentatomidae. Proceedings of the American Academy of Arts and Sciences 57(16): 391–422. https://doi.org/10.2307/20025937

Brunt AM (1971) The histology of the first batch of eggs and their associated tissues in the ovariole of *Dysdercus fasciatus* Signoret (Heteroptera: Pyrrhocoridae) as seen with the light microscope. Journal of Morphology 134(1): 105–129. https://doi.org/10.1002/jmor.1051340107

Bugaj-Nawrocka A, Chajec Ł, Urbisz AZ, Chłond D (2022) A microscopy investigation of the complex problem of infertility of insect hybrids. Studies on the reproductive systems, eggshells, and karyotypes of the representatives of the genus *Platymeris* (Heteroptera, Reduviidae) and their hybrids. Micron 158: e103248. https://doi.org/10.1016/j.micron.2022.103248

Büning J (1994a) The Insect Ovary. Ultrastructure, Previtellogenic Growth and Evolution. Chapman & Hall, London, 400 pp.

Büning J (1994b) The ovary of Ectognatha, the Insecta s. str. In: The Insect Ovary. Springer, Dordrecht, 31–324. https://doi.org/10.1007/978-94-011-0741-9_3

Candan S, Özyurt Koçakoğlu N, Suludere Z (2018) Morphological and histological structure of the male reproductive system of the water strider *Gerris lacustris* (Linnaeus 1758) (Gerridae, Heteroptera). Microscopy Research and Technique 81(7): 770–780. https://doi.org/10.1002/jemt.23035

Carayon J (1949) Observations sur la biologie des Hémiptères Microphysidae. Bulletin du Muséum National d'Histoire Naturelle 21(2): 710–716.

Carayon J (1950) Nombre et description des ovarioles dans les ovaries des Hémiptères -Hétéroptères. Bulletin du Muséum National d'Histoire Naturelle (2) 22(4): 470–75.

Carayon J (1951) Les organes genitaux males des Hemipteres Nabidae. Absence de symbiontes dans ces organes. Proceedings of the Royal Entomological Society of London (A) 26(1–3): 1–10. https://doi.org/10.1111/j.1365-3032.1951.tb00103.x

Carayon J (1954) Organes assumant les fonctions de la spermathèque chez divers Heteropteres. Bulletin de la Société Zoologique de France 79: 189–197.

Carayon J (1955) Quelques caractères anatomiques des Hémiptères Aradidés. Revue Française d'Entomologie 22: 169–180.

Carayon J (1972) Caractères Systématiques et classification des Anthocoridae (Hemiptera). Annales de la Société entomologique de France (N.S.) 8: 309–349.

Cassis G, Schuh RT (2012) Systematics, Biodiversity, Biogeography, and Host Associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha). Annual Review of Entomology 57(1): 377–404. https://doi.org/10.1146/annurev-ento-121510-133533

Cassis G, Schuh RT, Brailovsky H (1999) A review of *Onymocoris* (Heteroptera: Thaumastocoridae), with a new species, and notes on hosts and distributions of other thaumastocorid species. Acta Societatis Zoologicae Bohemicae 63(1–2): 19–36.

Chapman RF, Simpson SJ, Douglas AE (2013) The Insects: Structure and Function. 5th ed. Cambridge University Press, New York, 788 pp. [Chapter 12, 282–312: male; Chapter 13, 313–343: female] https://doi.org/10.1017/CBO9781139035460

Chen P-p, Nieser N, Zettel H (2005) The Aquatic and Semi-Aquatic bugs (Heteroptera: Nepomorpha & Geomorpha) of Malesia. Fauna Malesiana Handbook 5. Brill, Leiden, 546 pp. https://doi.org/10.1163/9789047416807

Chiang RG (2010) Functional anatomy of the vagina muscles in the adult western conifer seed bug, *Leptoglossus occidentalis* (Heteroptera: Coreidae), and its implication for the egg laying behaviour in insects. Arthropod Structure & Development 39(4): 261–267. https://doi.org/10.1016/j.asd.2010.02.004

Chiang RG, Chiang JA, Sarquis O, Lima MM (2012) Morphology of reproductive accessory glands in eight species of blood-feeding Hemiptera (Hemiptera, Reduviidae) insect vectors of Chagas disease. Acta Tropica 122(2): 196–204. https://doi.org/10.1016/j.actatropica.2012.01.011

Chiang RG, Chiang JA, Hoogendoorn H, Lima MM (2013) Exploring the role of rhodtestolin, a cardio-inhibitor from the testes of *Rhodnius prolixus*, in relation to the structure and function of reproductive organs in insect vectors of Chagas disease. Insects 4(4): 593–608. https://doi.org/10.3390/insects4040593

Coreoidea SF Team (2019) SF Coreoidea: Coreoidea Species File (version 5.0, Jun 2018). In: Species 2000 & ITIS Catalogue of Life, 2019 Annual Checklist. Roskov Y, Ower G, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, Nieukerken E van, Zarucchi J, Penev L, (Eds) Digital resource at www.catalogueoflife.org/annual-checklist/2019. Species 2000: Naturalis, Leiden, the Netherlands.

Couturier G, Do Socorro M, De Oliveira P, Beserra P, Pluot-Sigwalt D, Kahn F (2002) Biology of *Discocoris drakei* (Hemiptera: Thaumastocoridae) on *Oenocarpus mapora* (Palmae). The Florida Entomologist 85(1): 261–266. https://doi.org/10.1653/0015-4040(2002)085[0261:BODDHT]2.0.CO;2

Cremonez PSG, de Oliveira Pinheiro D, Falleiros ÂMF, Neves PMOJ (2017) Performance of reproductive system of *Dichelops melacanthus* (Hemiptera: Pentatomidae) subjected to buprofezin and pyriproxyfen: morphological analysis of ovarioles and testes. Semina. Ciências Agrárias 38(4): 2279–2291. https://doi.org/10.5433/1679-0359.2017v38n4SUPLp2279

Cremonez PSG, Gouvea SP, Pinheiro DO, Falleiros ÂMF, Levy SM, Meneghin AM, Fonseca ICB, Neves PMOJ (2019) Chitin Biosynthesis Inhibitors in *Euschistus heros* Fabr.

(Hemiptera: Pentatomidae): Morphometric Alterations in Testes and Nuclei of Testicular Accessory Cells of Adults. Journal of Agricultural Science 11(1): 410–417. https://doi.org/10.5539/jas.v11n1p410

Cryan JR, Urban JM (2012) Higher-level phylogeny of the insect order Hemiptera: Is Auchenorrhyncha really paraphyletic? Systematic Entomology 37(1): 7–21. https://doi.org/10.1111/j.1365-3113.2011.00611.x

Damgaard J (2008) Phylogeny of the semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha). Insect Systematics & Evolution 39(4): 431–460. https://doi.org/10.1163/187631208788784264

Damgaard C (2012) Trend analyses of hierarchical pin-point cover data. Ecology 93(6): 1269–1274. https://doi.org/10.1890/11-1499.1

Davis NT (1955) Morphology of the Female Organs of Reproduction in the Miridae (Hemiptera). Annals of the Entomological Society of America 48(3): 132–150. https://doi.org/10.1093/aesa/48.3.132

Davis NT (1956) The morphology and functional anatomy of the male and female reproductive systems of *Cimex lectularius* L. (Heteroptera, Cimicidae). Annals of the Entomological Society of America 49(5): 466–493. https://doi.org/10.1093/aesa/49.5.466

Davis NT (1966) Contributions to the morphology and phylogeny of the Reduvioidea (Hemiptera: Heteroptera) Part III. The male and female genitalia. Annals of the Entomological Society of America 59(5): 911–924. https://doi.org/10.1093/aesa/59.5.911

Davis NT, Usinger RL (1970) The biology and relationships of the Joppeicidae (Heteroptera). Annals of the Entomological Society of America 63(2): 577–587. https://doi.org/10.1093/aesa/63.2.577

Drake CJ, Davis NT (1960) The morphology, phylogeny, and higher classification of the family Tingidae, including the description of a new genus and species of the subfamily Vianaidinae (Hemiptera: Heteroptera). Entomologica Americana 39: 1–100.

Dufour JML (1833) Recherches anatomiques et physiologiques sur les hémiptères: accompanées de considérations relatives à l'histoire naturelle et à la classification des ces insectes. Impr de Bachelier, Paris. Extracted from Mémoires présentés par divers savants à l'Académie royale des sciences de l'Institut de France et imprimés par son ordre. Sciences mathématiques et physiques 4: 131–461. https://doi.org/10.5962/bhl.title.34925

Elelimy HAS, Ghazawy NA, Omar AH, Meguid AA (2017a) Morphology and histology of the male reproductive system of *Spilostethus pandurus* (Scopoli) (Hemiptera: Lygaeidae). African Entomology 25(1): 210–219. https://doi.org/10.4001/003.025.0210

Elelimy HAS, Ghazawy NA, Omar AH, Meguid AA (2017b) Morphology, histology and ovary development of the female reproductive system of *Spilostethus pandurus* (Scopoli) (Hemiptera: Lygaeidae). African Entomology 25(2): 515–522. https://doi.org/10.4001/003.025.0515

Esquivel JF (2009) Stages of Gonadal Development of the Southern Green Stink Bug (Hemiptera: Pentatomidae): Improved Visualization. Annals of the Entomological Society of America 102(2): 303–309. https://doi.org/10.1603/008.102.0212

Freitas SPC, Gonçalves TCM, Serrão JE, Santos-Mallet JR (2007a) Fine structure of the male accessory glands of *Triatoma rubrofasciata* (De Geer, 1773) (Hemiptera, Triatominae). Microscopy Research and Technique 70(4): 355–360. https://doi.org/10.1002/jemt.20419

Freitas SPC, Dos Santos-Mallet JR, Serrão JE, Lorosa ES, Gonçalves TCM (2007b) Morphometry of the testis follicles in *Triatoma rubrofasciata* (De Geer, 1773) (Hemiptera, Triatominae). Animal Biology 57(4): 393–400. https://doi.org/10.1163/157075607782232125

Freitas S, Santos-Mallet J, Costa J, Souza AL, Serrão J, Gonçalves T (2008) A comparative study of testis follicles in species of *Triatoma* (Hemiptera, Triatominae). Animal Biology 58(2): 227–233. https://doi.org/10.1163/157075608X328062

Freitas SPC, Gonçalves TCM, Serrão JE, Costa J, Santos-Mallet JR (2010) Male reproductive system structure and accessory glands ultrastructure of two species of *Triatoma* (Hemiptera, Reduviidae, Triatominae). Micron 41(5): 518–525. https://doi.org/10.1016/j.micron.2010.01.008

Freitas SPC, Bonifácio SF, Junqueira ÂC, Souza AL, Gonçalves TC (2012) Testicular and color variation in the kissing bug, *Rhodnius brethesi*, in Amazonas, Brazil. Journal of Insect Science 12(1): 65. https://doi.org/10.1673/031.012.6501

Gapon DA, Kuznetsova VG, Maryańska-Nadachowska A (2021) A new species of the genus *Rhaphidosoma* Amyot et Serville, 1843 (Heteroptera, Reduviidae), with data on its chromosome complement. Comparative Cytogenetics 15(4): 467–505. https://doi.org/10.3897/CompCytogen.v15.i4.78718

Gelbič I, Šula J, Socha R (1991) (R, S)-9-(2, 3-dihydroxypropyl) adenine induced sterility in females of the red cotton bug, *Dysdercus cingulatus* F. (Heteroptera, Pyrrhocoridae). Journal of Applied Entomology 111(1–5): 254–262. https://doi.org/10.1111/j.1439-0418.1991.tb00321.x

Golub NV, Golub VB, Anokhin BA, Kuznetsova VG (2022) Comparative Cytogenetics of Lace Bugs (Tingidae, Heteroptera): New Data and a Brief Overview. Insects 13(7): 608. https://doi.org/10.3390/insects13070608

Gomes MO, Castanhole MMU, Souza HV, Murakami AS, Firmino TSS, Saran PS, Bahno CA, Monteiro LS, Silva JCP, Itoyama MM (2013) Morphological aspects of the testes of 18 species of terrestrial Heteroptera from Northwestern São Paulo (Brazil). Biota Neotropica 13(3): 131–135. https://doi.org/10.1590/S1676-06032013000300016

Gonçalves TCM, Lent H, Almeida JRD (1987) Anatomic and morphometric studies of testicular follicles of some species of Triatominae (Hemiptera: Reduviidae). Memorias do Instituto Oswaldo Cruz 82(4): 543–550. https://doi.org/10.1590/S0074-02761987000400012 [MIOC]

Grimaldi D, Engel MS (2005) Evolution of the Insects. Cambridge University Press, Cambridge/ New York, NY, USA, 733 pp.

Grodowitz MJ, Reed DA, Elliott B, Perring TM (2019) Female Reproductive System Morphology and the Development of a Physiological Age-Grading System for *Bagrada hilaris* (Hemiptera: Pentatomidae). Journal of Insect Science 19(2): 15. [1–9] https://doi.org/10.1093/jisesa/iez022

Grodowitz MJ, Elliot B, Evans R, Rojas G, Morales-Ramos JA (2020) Development of a Physiological Age-Grading System for *Nezara viridula* (Hemiptera: Pentatomidae). Journal of Insect Science 20(5): 6. [1–8] https://doi.org/10.1093/jisesa/ieaa092

Gross J (1901) Untersuchungen iiber das Ovarium der Hemipteren, zugleich ein Beitrag zur Amitosenfrage. Zeitschrift für Wissenschaftliche Zoologie 69: 139–201.

Grozeva SM (1995) Karyotypes, male reproductive system, and abdominal trichobothria of the Berytidae (Heteroptera) with phylogenetic considerations. Systematic Entomology 20(3): 207–216. https://doi.org/10.1111/j.1365-3113.1995.tb00092.x

Grozeva S (2003) Karyotype of three endemic Mediterranean Miridae species (Heteroptera) from Bulgaria. Acta Zoologica Bulgarica 10(3): 19–27.

Grozeva S (2007) Cytogenetic data on five mezirine species (Heteroptera, Aradidae, Mezirinae). Annales of the Shumen University Konstantin Preslavski. Notulae Scientia Biologicae 17B(3): 18–26.

Grozeva S, Kuznetsova VG (1989) Karyotypes and some peculiarities of the reproductive system in the bugs from subfamily Artheneinae (Heteroptera, Pentatomomorpha, Lygaeidae). Entomologicheskoe Obozrenie 4: 700–709. [in Russian]

Grozeva S, Kuznetsova VG (1992) The reproductive system of some bug families (Heteroptera, Pentatomorpha). In: Bennettova B, Gelbic I, Soldan T (Eds) Advances in regulation of insect reproduction. Institute of Entomology, Czech Academy of Sciences, České Budějovice, 97–102.

Grozeva S, Nokkala S (1996) Chromosomes and their meiotic behavior in two families of the primitive infraorder Dipsocoromorpha (Heteroptera). Hereditas 125(1): 31–36. https://doi.org/10.1111/j.1601-5223.1996.t01-1-00031.x

Grozeva S, Nokkala S (2001) Chromosome numbers, sex determining systems, and patterns of the C-heterochromatin distribution in 13 species of lace bugs (Heteroptera, Tingidae). Folia Biologica 49(1/2): 29–42.

Grozeva SM, Simov NP (2008) Cytogenetic studies of Bryocorinae Baerensprung, 1860 true bugs (Heteroptera: Miridae). Acta Zoologica Bulgarica (Suppl. 2): 61–70.

Grozeva S, Nokkala S, Simov N (2006) First evidence of sex chromosomes pre-reduction in male meiosis in the Miridae bugs (Heteroptera). Folia Biologica 54(1–2): 9–12. https://doi.org/10.3409/173491606777919166

Grozeva S, Simov N, Josifov M (2007) Karyotaxonomy of some European *Macrolophus* species (Heteroptera, Miridae). Mainzer Naturwissenschaftliches Archiv (Beiheft 31): 81–87.

Grozeva S, Simov N, Nokkala S (2008) Achiasmatic male meiosis in three *Micronecta* species (Heteroptera: Nepomorpha: Micronectidae). Comparative Cytogenetics 2(1): 73–78.

Grozeva S, Nokkala S, Simov N (2009) Chiasmate male meiosis in six species of water bugs from infraorders Nepomorpha and Gerromorpha (Insecta, Heteroptera). Comparative Cytogenetics 3(2): 125–131. https://doi.org/10.3897/compcytogen.v3i2.19

Grozeva S, Kuznetsova V, Simov N, Langourov M, Dalakchieva S (2013) Sex chromosome pre-reduction in male meiosis of *Lethocerus patruelis* (Stål, 1854) (Heteroptera, Belostomatidae) with some notes on the distribution of the species. In: Popov A, Grozeva S, Simov N, Tasheva E (Eds) Advances in Hemipterology. ZooKeys 319: 119–135. https://doi.org/10.3897/zookeys.319.4384

Grozeva S, Kuznetsova V, Hartung V (2014) First cytogenetic study of Coleorrhyncha: Meiotic complement of *Xenophyes cascus* (Hemiptera: Peloridiidae). European Journal of Entomology 111(2): 303–306. https://doi.org/10.14411/eje.2014.023

Hagan HR (1931) The embryology of the polyctenid, *Hesperoctenes fumarus* Westwood, with refences to viviparity in insects. Journal of Morphology and Physiology 51(1): 1–117. https://doi.org/10.1002/jmor.1050510102

Hebsgaard MB, Andersen NM, Damgaard J (2004) Phylogeny of the true water bugs (Nepomorpha: Hemiptera-Heteroptera) based on 16S and 28S rDNA and morphology. Systematic Entomology 29(4): 488–508. https://doi.org/10.1111/j.0307-6970.2004.00254.x

Heiss E (2001) Superfamily Aradoidea Brulle´1836. In: Aukema B, Rieger C (Eds) Catalogue of the Heteroptera of the palaearctic region. Vol. 4. Netherlands Entomological Society, Amsterdam, 3–34.

Heming-van Battum KE, Heming BS (1986) Structure, function and evolution of the reproductive system in females of *Hebrus pusillus* and *Hebrus ruficeps* (Hemiptera, Gerromorpha, Hebridae). Journal of Morphology 190(2): 121–167. https://doi.org/10.1002/jmor.1051900202

Heming-van Battum KE, Heming BS (1989) Structure, function and evolutionary significance of the reproductive system in females of *Hebrus ruficeps* and *H. pusillus* (Hemiptera, Gerromorpha, Hebridae). Journal of Morphology 202(3): 281–323. https://doi.org/10.1002/jmor.1052020302

Henry TJ (1997a) Phylogenetic analysis of the family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. Annals of the Entomological Society of America 90(3): 275–301. https://doi.org/10.1093/aesa/90.3.275

Henry TJ (1997b) Cladistic analysis and revision of the stilt bug genera of the world (Heteroptera: Berytidae). Contributions of the American Entomological Institute 30(1): 1–100.

Henry TJ (1997c) Monograph of the stilt bugs, or Berytidae (Heteroptera), of the Western Hemisphere. Memoirs of the Entomological Society of Washington 19: 1–149.

Henry TJ (2009) Biodiversity of Heteroptera. In: G Foottit, PH Adler (Eds) Insect Biodiversity: Science and Society. Blackwell Publishers, London, 223–263. https://doi.org/10.1002/9781444308211.ch10

Henry TJ, Dellapé PM, Ferreira PSF (2015) The big-eyed bugs, chinch bugs, and seed bugs (Lygaeoidea). In: Panizzi A, Grazia J (Eds) Heteroptera of the Neotropics. Springer, Dordrecht, 459–519. https://doi.org/10.1007/978-94-017-9861-7_16

Horton DR, Lewis TM (2011) Variation inmale and female genitalia among ten species of North American *Anthocoris* (Hemiptera: Heteroptera: Anthocoridae). Annals of the Entomological Society of America 104(6): 1260–1278. https://doi.org/10.1603/AN11087

Hua J, Li M, Dong P, Cui Y, Xie Q, Bu W (2009) Phylogenetic analysis of the true water bugs (Insecta: Hemiptera: Heteroptera: Nepomorpha): evidence from mitochondrial genomes. BMC Evolutionary Biology 9(1): 134. https://doi.org/10.1186/1471-2148-9-134

Huebner E, Anderson E (1972) A cytological study of the ovary of *Rhodnius prolixus*. III. Cytoarchitecture and development of the trophic chamber. Journal of Morphology 138(1): 1–39. https://doi.org/10.1002/jmor.1051380102

Hunt C, Stebbing H (1992) High molecular weight microtubule-associated proteins within testes of hemipteran insects. Cell Biology International Reports 16(5): 465–474. https://doi.org/10.1016/S0309-1651(06)80065-2

Hwang WS, Weirauch C (2012) Evolutionary History of Assassin Bugs (Insecta: Hemiptera: Reduviidae): Insights from Divergence Dating and Ancestral State Reconstruction. PLoS ONE 7(9): e45523. https://doi.org/10.1371/journal.pone.0045523

Jahnke SM, Redaelli LR, Diefenbach LMG (2006) Internal reproductive organs of *Cosmoclopius nigroannulatus* (Hemiptera: Reduviidae). Brazilian Journal of Biology 66(2a, 2A): 509–512. https://doi.org/10.1590/S1519-69842006000300017

Jansson A, Scudder GGE (1974) The life cycle and sexual development of *Cenocorixa* species (Hemiptera, Corixidae) in the Pacific Northwest of North America. Freshwater Biology 4(1): 73–92. https://doi.org/10.1111/j.1365-2427.1974.tb00940.x

Jawale SM, Ranade DR (1990) Morphology of the ovaries of *Sphaerodema* (Diplonychus) rusticum (Heteroptera, Belostomatidae). Journal of Morphology 205(2): 183–192. https://doi.org/10.1002/jmor.1052050207

Jessop L (1983) A review of the genera of Plataspidae (Hemiptera) related to *Libyaspis*, with a revision of Cantharodes. Journal of Natural History 17(1): 31–62. https://doi.org/10.1080/00222938300770031

Johnson KP, Dietrich CH, Friedrich F, Beutel R, Wipfler B, Peters RS, Allen J, Petersen M, Donath A, Walden KKO, Kozlov A, Podsiadlowski L, Mayer C, Meusemann K, Vasilikopoulos A, Waterhouse R, Cameron S, Weirauch C, Swanson D, Percy D, Hardy N, Terry I, Liu S, Zhou S, Misof B, Robertson HM, Yoshizawa K (2018) Phylogenomics and the evolutionary history of hemipteroid insects. Proceedings of the National Academy of Sciences of the United States of America 115(50): 12775–12780. https://doi.org/10.1073/pnas.1815820115

Jung S, Kim H, Yamada K, Lee S (2010) Molecular phylogeny and evolutionary habitat transition of the flower bugs (Heteroptera: Anthocoridae). Molecular Phylogenetics and Evolution 57(3): 73–83. https://doi.org/10.1016/j.ympev.2010.09.013

Jyoti G, Santosh N, Ashok D (2015) Revamp Studies on Morpho-Histology of the Male Reproductive System of *Halys dentatus* Fabricius (Hemiptera: Pentatomidae). Annual Research & Review in Biology 6(3): 176–183. https://doi.org/10.9734/ARRB/2015/14941

Kauffman T (1971) Ecology, biology and gonad morphology of *Gerris rufoscutellatus* (Hemiptera: Gerridae) in Fairbanks, Alaska. American Midland Naturalist 86(2): 407–416. https://doi.org/10.2307/2423633

Kaufmann T (1966) Notes on the life history and morphology of *Calidea dregii* (Hemiptera: Pentatomidae: Scutellerini) in Ghana, West Africa. Annals of the Entomological Society of America 59(4): 654–659. https://doi.org/10.1093/aesa/59.4.654

Kaur H, Patial N (2012) Internal male reproductive organs in ten species of Heteroptera (Insecta: Hemiptera). Indian Journal of Fundamental and Applied Life Sciences 2(1): 317–324.

Kaur H, Patial N (2016) Internal male reproductive organs in five species of Heteroptera (Insecta: Hemiptera). Indian Journal of Fundamental and Applied Life Sciences 6(3): 30–35.

Kerkis J (1926) Zur Kenntnis des inneren Geschlechtsapparates der wasserbewohnender Hemiptera-Heteroptera. Revue Russe d'Entomologie 20: 296–307.

Kerzhner IM (1981) Heteroptera of the Family Nabidae. Fauna of the USSR. Bugs. Vol. 13(2). Academy of Sciences USSR, Zoological Institute, Nauka, Leningrad, 326 pp. [In Russian]

Kerzhner IM (1996) Family Nabidae. In: Aukema B, Rieger C (Eds) Catalogue of the Heteroptera of the Palaearctic Region, 2: 84–107. Netherlands Entomological Society.

Khandelwal B, Gupta YC, Mahour K (2019) Description of Reproductive System of Indian Water Scorpion, *Laccotrephes maculatus* Fabr. (Hemiptera, Heteroptera: Nepidae). Journal of Advanced Laboratory Research in Biology 10(3): 755–762.

Kirkpatrick TW (1937) Studies on the ecology of coffee plantations in East Africa-II. The autecology of *Antestia* spp. (Pent.) with a particular account of a strepsipterous parasite. The Transactions of the Entomological Society of London 86(14): 247–343. https://doi.org/10.1111/j.1365-2311.1937.tb00245.x

Klowden MJ (2013) Physiological Systems in Insects. Academic Press, Cambridge, MA, 696 pp. https://doi.org/10.1016/B978-0-12-415819-1.00001-5

Knyshov A, Weirauch C, Hoey-Chamberlain R (2021) Phylogenetic relationships and revised classification of the true bug infraorder Dipsocoromorpha (Insecta: Hemiptera: Heteroptera). Cladistics 37(3): 248–275. https://doi.org/10.1111/cla.12435

Koçakoğlu NÖ, Candan S, Suludere Z (2019) Notes on the morphology and histology of the ovarioles of *Gerris lacustris* (L.) (water strider) (Insecta: Hemiptera: Heteroptera: Gerridae). Zoologischer Anzeiger 278: 84–89. https://doi.org/10.1016/j.jcz.2018.12.001

Konstantinov F, Namyatova A, Cassis G (2018) A synopsis of the bryocorine tribes (Heteroptera: Miridae: Bryocorinae): Key, diagnoses, hosts and distributional patterns. Invertebrate Systematics 32(4): 866–889. https://doi.org/10.1071/IS17087

Koutsogeorgiou EI, Kouloussis NA, Koveos DS, Andreadis SS (2022) Females of *Halyomorpha halys* (Hemiptera: Pentatomidae) Experience a Facultative Reproductive Diapause in Northern Greece. Insects 13: 866. https://doi.org/10.3390/insects

Kugler JM, Rübsam R, Trauner J, Büning J (2006) The larval development of the telotrophic meroistic ovary in the bug *Dysdercus intermedius* (Heteroptera, Pyrrhocoridae). Arthropod Structure & Development 35(2): 99–110. https://doi.org/10.1016/j.asd.2005.12.001

Kullenberg B (1947) Uber Morphologie und Funktion des Kopulationsapparats der Capsiden und Nabiden. Zoologiska bidrag från Uppsala 24: 217–418.

Kumar R (1962) Morpho-taxonomical studies on the genitalia and salivary glands of some Pentatomoidea. Entomologisk Tidskrift 83(1): 44–88.

Kumar R (1964) Anatomy and relationships of Thaumastocoridae (Hemiptera: Cimicoidea). Australian Journal of Entomology 3(1): 48–51. https://doi.org/10.1111/j.1440-6055.1964.tb00621.x

Kumar R (1965) Contributions to the morphology and relationships of Pentatomoidea (Hemiptera: Heteroptera). Part I. Scutelleridae. Australian Journal of Entomology 4(1): 41–55. https://doi.org/10.1111/j.1440-6055.1965.tb00647.x

Kumar R (1967) Morphology of the reproductive and alimentary systems of the Aradoidea (Hemiptera), with comments on relationships within the superfamily. Annals of the Entomological Society of America 60(1): 17–25. https://doi.org/10.1093/aesa/60.1.17

Kumar R (1969) Morphology and relationships of the Pentatomoidea (Heteroptera). III Natalicolinae and some Terarotominae of uncertain position. The Entomological Society of America 62(4): 681–695. https://doi.org/10.1093/aesa/62.4.681

Kuznetsova V, Grozeva S, Nokkala S (2004) New cytogenetic data on Nabidae (Heteroptera, Cimicomorpha), with a discussion of karyotype variation and meiotic patterns, and their taxonomic significance. European Journal of Entomology 101(2): 205–210. https://doi.org/10.14411/eje.2004.026

Kuznetsova VG, Grozeva S, Sewlal JAN, Nokkala S (2007) Cytogenetic characterization of the Trinidad endemic, *Arachnocoris trinitatus* Bergroth: the first data for the tribe Arachnocorini (Heteroptera: Cimicomorpha: Nabidae). Folia Biologica 55(1–2): 17–26. https://doi.org/10.3409/173491607780006344

Kuznetsova VG, Grozeva SM, Hartung V, Anokhin BA (2015) First evidence for (TTAGG)n telomeric sequence and sex chromosome post-reduction in Coleorrhyncha (Insecta, Hemiptera). Comparative Cytogenetics 9(4): 523–532. https://doi.org/10.3897/CompCytogen.v9i4.5609

Lalitha TG, Shyamasundari K, Hanumantha Rao K (1997) Morphology and histology of the female reproductive system of *Abedus ovatus* Stål (Belostomatidae: Hemiptera: Insecta). Memorias do Instituto Oswaldo Cruz 92(1): 129–135. https://doi.org/10.1590/S0074-02761997000100028

Larivière M-C, Larochelle A (2019) World Saldidae: Supplement 1987–2018) to the catalog and bibliography of the Leptopodomorpha (Heteroptera). Zootaxa 4590(1): 125–152. https://doi.org/10.11646/zootaxa.4590.1.5

Larsen O (1938) Untersuchungen über den Geschlechtsapparat der aquatilen Wanzen. Opuscula Entomologica (Supplement 1): 1–388.

Lemos WP, Serrão JE, Ramalho FS, Zanuncio JC, Lacerda MC (2005a) Effect of diet on male reproductive tract of *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae). Brazilian Journal of Biology 65(1): 91–96. https://doi.org/10.1590/S1519-69842005000100012

Lemos W, de Souza Ramalho F, Serrão JE, Zanuncio JC (2005b) Morphology of female reproductive tract of the predator *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) fed on different diets. Brazilian Archives of Biology and Technology 48(1): 129–138. https://doi.org/10.1590/S1516-89132005000100017

Lemos WP, Zanuncio VV, Ramalho FS, Zanuncio JC, Serrão JE (2010) Ovary histology of the predator *Brontocoris tabidus* (Hemiptera: Pentatomidae) of two ages fed on different diets. Entomological News 121(3): 230–235. https://doi.org/10.3157/021.121.0303

Lent H, Jurberg J, Galvão C (1994) Revalidação do gênero *Mepraia* Mazza, Gajardo & Jorg, 1940 (Hemiptera, Reduviidae, Triatominae). Memorias do Instituto Oswaldo Cruz 89(3): 347–352. https://doi.org/10.1590/S0074-02761994000300008

Leston D (1961a) Testis follicle number and the higher systematics of Miridae (Hemiptera-Heteroptera). Proceedings of the Zoological Society of London 137(1): 89–106. https://doi.org/10.1111/j.1469-7998.1961.tb06163.x

Leston D (1961b) The Number of testis follicles in Miridae. Nature 4783(4783): 93. https://doi.org/10.1038/191093a0

Leston D, Gibbs DG (1968) A new Deraeocorine (Hemiptera: Miridae) predacious on *Mesohomotoma tessmanni* (Aulmann) (Hemiptera: Psyllidae) on cocoa. Proceedings of the Royal Entomological Society of London, Series B, Taxonomy [Oxford, UK: Blackwell Publishing Ltd.] 37(5–6): 73–79. https://doi.org/10.1111/j.1365-3113.1968.tb00200.x

Lis JZ (2003) Ovaries and lateral oviducts of the female internal reproductive system in five species of burrower bugs (Hemiptera: Heteroptera: Cydnidae). Polish Journal of Entomology 72: 305–312.

Lis EA, Bulińska-Balas M, Lis P, Ziala, Kocorek A (2012) Systematic position of Dinidoridae and Tessaratomidae within the superfamily Pentatomoidea (Hemiptera: Heteroptera) based on the analysis of the mitochondrial cytochrome oxidase II sequences. Nature Journal 45: 43–54.

Liu Y, Li H, Song F, Zhao Y, Wilson JJ, Cai W (2019) Higher-level phylogeny and evolutionary history of Pentatomomorpha (Hemiptera: Heteroptera) inferred from mitochondrial genome sequences. Systematic Entomology 44(4): 810–819. https://doi.org/10.1111/syen.12357

Louis D, Kumar R (1973) Morphology of the alimentary and reproductive organs in Reduviidae (Hemiptera: Heteroptera) with comments on interrelationships within the family. Annals of the Entomological Society of America 66(3): 635–639. https://doi.org/10.1093/aesa/66.3.635

Ludwig W (1926) Untersuchungen űber den Copulations-apparat der Baumwanzen. Zeitschrift für Morphologie und Ökologie der Tiere 6(2): 291–380. https://doi.org/10.1007/BF00408030

Lung KYH, Goeden RD (1982) Biology of Corimelaena extensa on tree tobacco, *Nicotiana glauca*. Annals of the Entomological Society of America 75(2): 177–180. https://doi.org/10.1093/aesa/75.2.177

Ma WK, Ramaswamy SB (1987) Histological changes during ovarian maturation in the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae). International Journal of Insect Morphology & Embryology 16(5–6): 309–322. https://doi.org/10.1016/0020-7322(87)90003-1

Maddison WP, Maddison DR (2018) Mesquite: a modular system for evolutionary analysis. Version 3.6. [WWW document] http://www.mesquiteproject.org/home.html [Accessed 22 Jun 2022]

Mahmood S, Amir M, Gupta R, Yasmeen S (2018) Histological effects of chlorpyrifos on the reproductive organs of red cotton stainer, *Dysdercus koenigii* (Fabricius) (Hemiptera: Pyrrhocoridae). Journal of Entomology and Zoology Studies 6(3): 01–05.

Malipatil MB (1978) Testis follicle and ovariole numbers in the Lygaeidae (Heteroptera). Entomologist's Monthly Magazine 113: 1352–1355.

Marchini D, Del Bene G, Dallai R (2009) Functional morphology of the female reproductive apparatus of *Stephanitis pyrioides* (Heteroptera, Tingidae): A novel role for the pseudospermathecae. Journal of Morphology 271(4): 473–482. https://doi.org/10.1002/jmor.10811

Marshall WS, Severin HHP (1903) Some points in the anatomy of *Ranatra fusca*. Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 14: 487–508.

Matsuda R (1976) Morphology and evolution of the insect abdomen. With special reference to developmental patterns and their bearings upon systematics. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt, 534 pp.

Miyamoto S (1957) List of ovariole numbers in Japanese Heteroptera. Sieboldia 2(1): 69–82.

Miyamoto S (1959) Additions and correction to my "List of ovariole numbers in Japanese Heteroptera". Sieboldia 2: 121–123.

Mróz E (2007) Anatomical and molecular studies of *Stenodema* Laporte genus (Heteroptera: Miridae). Genus 14: 77–81.

Mróz E (2012) The structure of the male reproductive system of the genus *Psallus* Fieber (Hemiptera: Heteroptera: Miridae). Polish journal of entomology 81(2): 107–118. https://doi.org/10.2478/v10200-011-0070-8

Mróz E, Wojciechowski W (2011) The systematic position of the tribe Stenodemini (Heteroptera: Cimicomorpha: Miridae: Mirinae) in the light of the male internal reproductive system. Journal of Natural History 45(25–26): 1563–1588. https://doi.org/10.1080/00222933.2011.559595

Munhoz ILA, Serrão JE, Dias G, Lino-Neto J, Melo AL, Araújo VA (2020) Anatomy and histology of the male reproductive tract in giant water bugs of the genus *Belostoma* Latreille, 1807 (Heteroptera, Belostomatidae). International Journal of Tropical Insect Science 40(2): 1608–1614. https://doi.org/10.1007/s42690-020-00207-7

Munhoz ILA, Serrao JE, Melo AL, Martins LCB, Araújo VA (2021) Anatomy and histology of the male reproductive tract in creeping water bugs (Heteroptera: Naucoridae). Acta Zoologica 103(4): 433–441. https://doi.org/10.1111/azo.12384

Nieser N (2002) Guide to aquatic Heteroptera of Singapore and Peninsular Malaysia. IV. Corixoidea. The Raffles Bulletin of Zoology 50(1): 263–274.

Novais AM, Dias G, Lino-Neto J (2017) Testicular, spermatogenesis and sperm morphology in *Martarega bentoi* (Heteroptera: Notonectidae). Arthropod Structure & Development 46(4): 635–643. https://doi.org/10.1016/j.asd.2017.04.002

Ogorzałek A (2007) Structural and functional diversification of follicular epithelium in *Coreus marginatus* (Coreidae: Heteroptera). Arthropod Structure & Development 36(2): 209–219. https://doi.org/10.1016/j.asd.2006.09.004

Ogorzałek A, Trochimczuk A (2009) Ovary structure in a presocial insect, *Elasmucha grisea* (Heteroptera, Acanthosomatidae). Arthropod Structure & Development 38(6): 509–519. https://doi.org/10.1016/j.asd.2009.08.001

Oliveira MS, Serrão JE, Dias G, Luiza Martins LCB, Araújo VA (2021) Anatomy and histology of the male reproductive tract of *Machtima crucigera* (Fabricius, 1775) (Heteroptera: Coreidae). Zoologischer Anzeiger 293: 156–162. https://doi.org/10.1016/j.jcz.2021.06.009

Özyurt N, Candan S, Suludere Z, Amutkan D (2013a) Morphology and histology of the male reproductive system in *Graphosoma lineatum* (Heteroptera: Pentatomidae) based on optical and scanning electron microscopy. Journal of Entomology and Zoology Studies 1(4): 40–46. https://doi.org/10.15373/22778179/DEC2013/14

Özyurt N, Candan S, Suludere Z (2013b) The morphology and histology of the male reproductive system in *Dolycoris baccarum* Linnaeus 1758 (Heteroptera: Pentatomidae) - Light and scanning electron microscope studies. Micron (Oxford, England) 44: 101–106. https://doi.org/10.1016/j.micron.2012.04.017

Özyurt N, Candan S, Suludere Z (2014a) Structure of the male reproductive system and spermatogenesis of *Codophila varia* (Fabricius, 1787) (Heteroptera: Pentatomidae) by light and scanning electron microscopy. Journal of Entomological Research Society 16(1): 101–110.

Özyurt N, Candan S, Suludere Z (2014b) The morphology and histology of the male reproductive system in *Apodiphus amygdali* (Germar, 1817) (Hemiptera: Heteroptera: Pentatomidae). Life: the Excitement of Biology 2(1): 31–41. https://doi.org/10.9784/LEB2(1)Ozyurt.01

Özyurt N, Candan S, Suludere Z (2015) Ultrastructure of male reproductive system of *Eurydema ventrale* Kolenati 1846 (Heteroptera: Pentatomidae). Microscopy Research and Technique 78(8): 643–653. https://doi.org/10.1002/jemt.22514

Papáček M, Gelbič I (1989) Development of the male internal reproductive system in the saucer bug (*Ilyocoris cimicoides* L.) (Heteroptera, Naucoridae). In: Tonner M, Soldán T, Bennettová B (Eds) Regulation of insect reproduction. IV. Proceedings of a symposium held in Žinkovy, September 1987, Academia, Praha, 125–140.

Papáček M, Soldán T (1992) Development of the male internal reproductive system in *Notonecta glauca* (Heteroptera, Notonectidae). In: Bennettová B, Gelbic I, Soldán T (Eds) Advances in Regulation of Insect Reproduction. Institute of Entomology. České Budějovice: Czech Academy of Science, 199–211.

Papáček M, Soldán T (2008) Structure and development of the reproductive system in *Aphelocheirus aestivalis* (Hemiptera: Heteroptera: Nepomorpha: Aphelocheiridae). Acta Entomologica Musei Nationalis Pragae 48(2): 299–318.

Papáček M, Zettel H (2005) Helotrephidae of the World (Hemiptera: Heteroptera: Nepomorpha): checklist and bibliography. Acta Societatis Zoologicae Bohemicae 68: 99–108.

Papáček M, Soldán T, Truhlářová I (1997) Development of the female internal reproductive system in *Ilyocoris cimicoides* (Heteroptera: Nepomorpha: Naucoridae). Acta Societatis Zoologicae Bohemicae 61(1): 77–84.

Payne MA (1934) Intravitam studies on the hemipteran, *Leptocoris trivittatus*. A description of the male reproductive organs and the aggregation and turning of the sperms. Journal of Morphology 56(3): 513–531. https://doi.org/10.1002/jmor.1050560305

Pendergrast JG (1956) The male reproductive organs of *Nezara viridula* (L.) with a preliminary account of their development (Heteroptera: Pentatomidae). Transactions of the Royal Society of New Zealand 34(1): 139–146.

Pendergrast JG (1957) Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. Transactions of the Royal Entomological Society of London 109(1): 1–63. https://doi.org/10.1111/j.1365-2311.1957.tb00133.x

Pereira LLV, Alevi KCC, Castanhole MM, Moreira FFF, Barborsa JF, Itoyama MM (2015) Cytogenetics analysis and testis morphology of aquatic species of the families Belostomatidae, Gelastocoridae, Gerridae, Notonectidae and Veliidae (Heteroptera). Journal of Insect Science 15(21): 1–10. https://doi.org/10.1093/jisesa/iev009

Perez-Goodwyn PJ (2006) Taxonomic revision of the subfamily Lethocerinae (Heteroptera: Belostomatidae). Stuttgarter Beiträge zur Naturkunde A 695: 1–71.

Péricart J (1972) Hémiptères: Anthocoridae, cimicidae et microphysidae de l'ouest-Paléarctique Faune de l'Europe et du bassin méditerranéen. Masson, Paris, 402 pp.

Péricart J (1996) Family Anthocoridae Fieber, 1836 – flower bugs, minute pirate bugs. In: Aukema B, Rieger C (Eds) Catalogue of the Heteroptera of the Palaearctic Region. The Netherland Entomological Society, Amsterdam 2: 108–140.

Pires EM, Ferreira PS, Guedes RN, Serrão JE (2007) Morphology of the phytophagous bug *Platyscytus decempunctatus* (Carvalho) (Heteroptera: Miridae). Neotropical Entomology 36(4): 510–513. https://doi.org/10.1590/S1519-566X2007000400004

Pluot-Sigwalt D, Chérot F (2013) Données biologiques et anatomiques, régime alimentaire et taxonomie d'un nouveau *Fulvius afrotropical* (Insecta, Heteroptera, Miridae, Cylapinae, Fulviini). Zoosystema 35(1): 45–68. https://doi.org/10.5252/z2013n1a5

Poisson R (1927) Recherches sur quelques processus spermatoliénéthlues observés dans les éléments sexuels jeunes de *Notonecta maculata* Fab. Archives de Zoologie Expérimentale et Générale 66: 23–70.

Polhemus JT, Polhemus DA (2008) Global diversity of true bugs (Heteroptera; Insecta) in freshwater. Hydrobiologia 595(1): 379–391. https://doi.org/10.1007/s10750-007-9033-1

Polhemus JT, Polhemus DA (2012) Guide to the aquatic Heteroptera of Singapore and peninsular Malaysia. IX. Infraorder Nepomorpha, families Ochteridae and Gelastocoridae. The Raffles Bulletin of Zoology 60: 343–359.

Popov YA (1971) Historical development of Heteroptera, Infraorder Nepomorpha. Trudy Paleontologicheskogo Instituta Akademii nauk SSSR, Vol. 129. Nauka, Moscow, 230 pp. [In Russian]

Postle AC, Woodward TE (1988) The digestive and male internal reproductive systems of some Australian Anthocoridae (Hemiptera). Journal of the Australian Entomological Society 27(2): 117–129. https://doi.org/10.1111/j.1440-6055.1988.tb01158.x

Rebagliati PJ, Mola LM, Papeschi AG, Grazia J (2005) Cytogenetic studies in Pentatomidae (Heteroptera): A review. Journal of Zoological Systematics and Evolutionary Research 43(3): 199–213. https://doi.org/10.1111/j.1439-0469.2005.00312.x

Ribeiro JRI, Rodrigues HDD, Barbosa JF (2018) Taxonomic Catalog of the Brazilian Fauna (TCBF). http://fauna.jbrj.gov.br/fauna/listaBrasil/ConsultaPublicaUC/ConsultaPublicaUC.do [Accessed 21/09/2-22]

Rider DA (2006) Family Pentatomidae. In: Aukema B, Rieger C (Eds) Catalogue of the Heteroptera of the Palaearctic Region. Vol. 5. The Netherlands Entomological Society, Amsterdam, 233–402.

Rider DA, Schwertner CF, Vilímová J, Rédei D, Kment P, Thomas DB (2018) Higher Systematics of the Pentatomoidea. In: McPherson JE (Ed.) Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management. CRC Press, Taylor & Francis Group, Boca Raton, London/New York, 25–201. https://doi.org/10.1201/9781315371221-2

Rolston LH, Aalbu RL, Murray MJ, Rider DA (1993) A catalog of the Tessaratomidae of the world. Papua New Guinea Journal of Agriculture, Forestry and Fisheries 36: 36–108.

Samanta J, Chakraborty S, Kanti Mukherjee T (2022) The Reproductive System of *Diplonychus rusticus* (Fabricius, 1781) (Belostomatidae: Hemiptera) with a Note on Feeding. Journal of the Bombay Natural History Society 119(January–April). [JBNHS]

Santos RSS, Redaelli LR, Diefenbach LMG, Romanowski HP, Prando HF, Antochevis RC (2005) Seasonal abundance and mortality of *Oebalus poecilus* (Dallas) (Hemiptera: Pentatomidae) in a hibernation refuge. Brazilian Journal of Biology 66(2a): 447–453. https://doi.org/10.1590/S1519-69842006000300010

Sarel-Whitfield FG (1929) The Sudan millet bug, *Agonoscelis versicolor* F. Bulletin of Entomological Research 20(2): 209–220. https://doi.org/10.1017/S0007485300021143

Schlee D (1969) Morphologie und Symbiose; ihre Beweiskraft für die Verwandtschaftsbeziehungen der Coleorrhyncha. Stuttgarter Beiträge zur Naturkunde 210: 1–27.

Schneider G (1940) Bierträge zur Kenntnis der Symbiontischen Einrichtungen der Heterpteren. Zeitschrift für Morphologie und Ökologie der Tiere 36(4): 595–643. https://doi.org/10.1007/BF01261001

Schrader F (1960a) Cytological and evolutionary implications of aberrant chromosome behavior in the harlequin lobe of some Pentatomidae (Heteroptera). Chromosoma 11(1): 103–128. https://doi.org/10.1007/BF00328648

Schrader F (1960b) Evolutionary aspects of aberrant meiosis in some Pentatominae (Heteroptera). Evolution; International Journal of Organic Evolution 14: 498–508. https://doi.org/10.1111/j.1558-5646.1960.tb03116.x

Schuh RT (1995) Plant bugs of the World (Heteroptera: Miridae): Systematic catalog, distributions, host list, and bibliography. New York Entomological Society, 1329 pp.

Schuh RT, Polhemus JT (1980) Analysis of taxonomic congruence among morphological, ecological and biogeographic data sets for the Leptopodomorpha (Hemiptera). Systematic Zoology 29(1): 1–26. https://doi.org/10.2307/2412623

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Cornell University Press, Ithaca, New York, 336 pp.

Schuh RT, Štys P (1991) Phylogenetic analysis of Cimicomorphan family relationships (Heteroptera). Journal of the New York Entomological Society 99(3): 298–350.

Schuh RT, Weirauch C (2020) True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. Siri Scientific Press, Rochdale, Monograph Series Vol. 8, 800 pp.

Schuh RT, Galil B, Polhemus JT (1987) Catalog and bibliography of Leptopodomorpha (Heteroptera). Bulletin of the American Museum of Natural History 185: 243–406.

Schuh RT, Weirauch C, Wheeler WC (2009) Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total-evidence analysis. Systematic Entomology 34(1): 15–48. https://doi.org/10.1111/j.1365-3113.2008.00436.x

Schwartz MD (2008) Revision of the Stenodemini with a review of the included genera (Hemiptera: Heteroptera: Miridae: Mirini). Proceedings of the Entomological Society of Washington 110(4): 1111–1201. https://doi.org/10.4289/0013-8797-110.4.1111

Scudder GGE (1957) The systematic position of *Dicranocephalus* Hahn, 1826 and its allies (Hemiptera: Heteroptera). Proceedings of the Royal Entomological Society (A) 32(10–12): 147–158. https://doi.org/10.1111/j.1365-3032.1957.tb00363.x

Simiczyjew B (1999) The ovary structure and oogenesis in *Hydrometra stagnorum* (Heteroptera: Hydrometridae). Acta Societatis Zoologicae Bohemicae 63: 187–197.

Simiczyjew B, Ogorzałek A, Štys P (1996) Organization of the trophic chamber in the telotrophic ovariole of *Nepa cinerea* and *Aradus pictus* (Hemiptera, Heteroptera). Zoologica Poloniae 41(1–4): 103–116.

Simiczyjew B, Ogorzałek A, Štys P (1998) Heteropteran ovaries: Variations on the theme. Folia Histochemica et Cytobiologica 36(4): 147–156.

Sites RW (2022) Phylogeny and revised classification of the saucer bugs (Hemiptera: Nepomorpha: Naucoridae). Zoological Journal of the Linnean Society 195(4): 1245–1286. https://doi.org/10.1093/zoolinnean/zlab105

Slack HD (1938) Cytological studies on five families of Hemiptera-Heteroptera. PhD Thesis, University of Edinburgh, UK.

Slater JA (1955) A revision of the subfamily Pachygronthinae of the World (Hemiptera: Lygaeidae). Philippine Journal of Science 84(1): 1–160.

Slater JA (1982) Hemiptera. In: Parker, SP (Ed.) Synopsis and Classification of Living Organisms. McGraw Hill Book Co., New York, 417–447.

Slater JA, Miyamoto S (1963) A revision of the sugar cane bugs of the genus *Cavelerius*. (Lygaeidae: Blissinae). Mushi 37: 139–154.

Socha R, Galbič I, Šula J (1988) Histopathological effects of (R, S)-9-(2, 3-dihydroxypropyl) adenine on ovaries of *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae). Acta Entomologica Bohemoslovaca 85: 408–417.

Soto A, Oliveira HG, Bacca T (2012) Morphology and histology of the reproductive system of *Supputius cincticeps* (Hemiptera: Heteroptera: Pentatomidae). Revista Udca Actualidad & Divulgacion Cientifica 15(1): 117–123. https://doi.org/10.31910/rudca.v15.n1.2012.808

Souza HV, Souza FB, Maruyama SRC, Castanhole MMU, Itoyama MM (2009) Meiosis, spermatogenesis and nucleolar behavior in the seminiferous tubules of Alydidae, Coreidae and Rhopalidae (Heteroptera) species. Genetics and Molecular Research 8(4): 1383–1396. https://doi.org/10.4238/vol8-4gmr672

Souza HV, Murakami AS, De Moura J, De Almeida EC, Marques IFG, Itoyama MM (2011) Comparative analysis of the testes and spermatogenesis in species of the family Pentatomidae (Heteroptera). European Journal of Entomology 108(3): 333–345. https://doi.org/10.14411/eje.2011.041

Souza GK, Pikart TG, Zanuncio TV, Wilcken CF, Serréo JE, Zanuncio JC (2014) Reproductive tract histology of *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae). Annals of the Entomological Society of America 107(4): 853–857. https://doi.org/10.1603/AN13061

Štys P (1970) On the morphology and classification of the family Dipsocoridae s. lat., with particular reference to the genus *Hypsipteryx* Drake (Heteroptera). Acta Entomologica Bohemoslovaca 67(1): 21–46.

Štys P (1971) Distribution and habitats of Joppeicidae (Heteroptera). Acta Entomologica Musei Nationalis Pragae 14: 199–208.

Štys P (1995a) Enicocephalomorpha. In: Schuh RT, Slater JA (Eds) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Comstock Publishing Associates, Cornell University Press, Ithaca/London, 67–73.

Štys P (1995b) Dipsocoromorpha. In: Schuh RT, Slater JA (Eds) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Comstock Publishing Associates, Cornell University Press, Ithaca/London, Journal of the New York Entomological Society 103: 74–83.

Štys P (2002) Key to the genus-group taxa of the extant Enicocephalomorpha of the world, their list, and taxonomic changes (Heteroptera). Acta Universitatis Carolinae. Biologica 45: 339–368.

Štys P, Baňař P (2008) *Xenicocephalus* – an enigmatic genus of American Enicocephalidae (Heteroptera): a new male-based species from Suriname. In: Grozeva S, Simov N (Eds) Advances in Heteroptera research. Festschrift in honor of the 80th anniversary of Michail Josifov. Pensoft, Sofia/Moscow, 357–376.

Štys P, Kerzhner IM (1975) The rank and nomenclature of higher taxa in recent Heteroptera. Acta Entomologica Bohemoslovaca 72(2): 65–79.

Štys P, Büning J, Biliński SM (1998) Organization of the tropharia in the telotrophic ovaries of the dipsocoromorphan bugs *Cryptostemma alienum* Herrich-Schaeffer and *C. carpaticum* Josifov (Heteroptera: Dipsocoridae). International Journal of Insect Morphology & Embryology 27(2): 129–133. https://doi.org/10.1016/S0020-7322(97)00025-1

Szentiványi T, Hornok S, Kovács ÁB, Takács N, Gyuranecz M, Markotter W, Christe P, Glaizot O (2022) Polyctenidae (Hemiptera: Cimicoidea) species in the Afrotropical region: Distribution, host specificity, and first insights to their molecular phylogeny. Ecology and Evolution 12(10): e9357. https://doi.org/10.1002/ece3.9357

Tatarnic NJ, Cassis G, Hochuli DF (2006) Traumatic insemination in the plant bug genus *Coridromius* Signoret (Heteroptera: Miridae). Biological Letters 2(1): 58–61. https://doi.org/10.1098/rsbl.2005.0394

Tsai JF, Redei D, Yeh GF, Yang MM (2011) Jewel Bugs of Taiwan (Heteroptera: Scutelleridae). National Chung Hsing University, Taichung, 309 pp.

Uceli LF, Pirovani VD, de Freitas Vicente NM, Pikart TG, Ferreira PSF, Serrao JE (2011) Morphology of the reproductive and digestive tracts of *Adparaproba gabrieli* (Heteroptera: Miridae). International Journal of Tropical Insect Science 31(4): 219–224. https://doi.org/10.1017/S1742758411000385

Usinger RL, Matsuda R (1959) Classification of the Aradidae. London, British Museum, 410 pp.

Van Doesburg PH, Cassis G, Monteith GB (2010) Discovery of a living fossil: a new xylastodorine species from New Caledonia (Heteroptera: Thaumastocoridae) and first record of the subfamily from the eastern Hemisphere. Zoölogische Mededeelingen 84: 93–115.

Vélez M, Dias G, Morales I, Guedes RNC, Lino-Neto J (2020) Morphology and histology of the male reproductive system of *Collaria oleosa* (Distant, 1883) (Heteroptera: Miridae). Revista Bionatura 5(2): 1122–1125. https://doi.org/10.21931/RB/20120.05.02.7

Wang YH, Cui Y, Rédei D, Baňař P, Xie Q, Štys P, Damgaard J, Chen PP, Yi WB, Wang Y, Dang K, Li C, Bu WJ (2016) Phylogenetic divergences of the true bugs (Insecta: Hemiptera: Heteroptera), with emphasis on the aquatic lineages: the last piece of the aquatic insect jigsaw originated in the Late Permian/Early Triassic. Cladistics 32(4): 390–405. https://doi.org/10.1111/cla.12137

Weirauch C (2008) Cladistic analysis of Reduviidae (Heteroptera: Cimicomorpha) based on morphological characters. Systematic Entomology 33(2): 229–274. https://doi.org/10.1111/j.1365-3113.2007.00417.x

Weirauch C, Munro JB (2009) Molecular phylogeny of the assassin bugs (Hemiptera: Reduviidae), based on mitochondrial and nuclear ribosomal genes. Molecular Phylogenetics and Evolution 53(1): 287–299. https://doi.org/10.1016/j.ympev.2009.05.039

Weirauch C, Schuh RT (2011) Systematics and evolution of Heteroptera: 25 years of progress. Annual Review of Entomology 56(1): 487–510. https://doi.org/10.1146/annurev-ento-120709-144833

Weirauch C, Bérenger J-M, Berniker L, Forero D, Forthman M, Frankenberg S, Freedman A, Gordon E, Hoey-Chamberlain R, Hwang WS, Marshall SA, Michael A, Paiero SM, Udah O, Watson C, Yeo M, Zhang G, Zhang J (2014) An illustrated identification key to assassin bug subfamilies and tribes (Hemiptera: Reduviidae). Canadian Journal of Arthropod Identification 26. https://doi.org/10.3752/cjai.2014.26

Weirauch C, Hoey-Chamberlai R, Knyshov A (2018) Synopsis of Schizopteridae (Hemiptera, Heteroptera, Dipsocoromorpha) from the United States, with description of seven new species from the US and Mexico. ZooKeys 796: 49–82. https://doi.org/10.3897/zookeys.796.24176

Weirauch C, Schuh RT, Cassis G, Wheeler WC (2019) Revisiting habitat and lifestyle transitions in Heteroptera (Insecta: Hemiptera): insights from a combined morphological and molecular phylogeny. Cladistics 35(1): 67–105. https://doi.org/10.1111/cla.12233

Wheeler WC, Schuh RT, Bang R (1993) Cladistic relationships among higher groups of Heteroptera: Congruence between morphological and molecular data sets. Insect Systematics & Evolution 24(2): 121–137. https://doi.org/10.1163/187631293X00235

Wightman JA (1973) Ovariole microstructure and vitellogenesis in *Lygocoris pabulinus* (L.) and other mirids (Hemiptera: Miridae). Journal of Entomology Series A, General Entomology 48(1): 103–115. https://doi.org/10.1111/j.1365-3032.1973.tb00042.x

Wille J (1929) Die Riibe Blattwanze, *Piesma quadrata* Fieb. Monographien zum Pflanzenschutz, Springer, Berlin, 2: 1–116.

Woodward TE (1949) The internal male reproductive organs in the genus *Nabis* Latreille (Nabidae: Hemiptera-Heteroptera). Proceedings of the Royal Entomological Society of London. Series A, General Entomology 24(10–12): 111–118. https://doi.org/10.1111/j.1365-3032.1949.tb00637.x

Woodward TE (1950) Ovariole and testis follicle numbers in the Heteroptera Entomologist's Monthly Magazine 86: 82–84.

Woodward TE (1977) The occurrence of Almeidini (Hemiptera: Anthocoridae) in Australia, with the description of a new genus. Systematic Entomology 2(3): 255–260. https://doi.org/10.1111/j.1365-3113.1977.tb00374.x

Wygodzinsky P (1955) Description of a new *Cryptostemma* from North America (Hemiptera: Cryptostemmatidae). The Pan-Pacific Entomologist 31: 199–202.

Wygodzinsky P (1966) A monograph of the Emesinae (Reduviidae, Hemiptera). Bulletin of the American Museum of Natural History 133: 1–614.

Xia Z, Li C (2019) The structure and morphological development of the reproductive system in *Corythucha marmorata* (Hemiptera: Tingidae). Huanjing Kunchong Xuebao 41(3): 574–580.

Xie Q, Tian Y, Zheng L-Y, Bu W-J (2008) 18S rRNA hyper-elongation and the phylogeny of Euhemiptera (Insecta: Hemiptera). Molecular Phylogenetics and Evolution 47(2): 463–471. https://doi.org/10.1016/j.ympev.2008.01.024

Ye Z, Damgaard J, Yang H, Hebsgaard B, Weir T, Bu W (2019) Phylogeny and diversification of the true water bugs (Insecta: Hemiptera: Heteroptera: Nepomorpha). Cladistics 36(1): 72–87. https://doi.org/10.1111/cla.12383

Supplementary material 1

An updated list of testicular follicles' and ovarioles' numbers in Heteroptera

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Data type: Morphological data

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